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THE UTILITY OF THE AIR BLADDER POSITION IN DETERMINING SPECIFIC RELATIONSHIPS IN THE ATHERINID GENUS *MENIDIA*

Robert J. Edwards, Edie Marsh and Fred B. Stevens, Jr.[1]

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Variation in the posterior extension of the air bladder, as measured by the number of anal fin rays plus the anal spine observed beneath it, was investigated in populations of *Menidia beryllina* in Texas. This character was found to vary inversely with salinity with the greatest intrapopulation variation occurring at intermediate salinities. The posterior position of the air bladder was manipulated experimentally by short-term changes in salinity and formalin concentration. This character has been used by various authors as a taxonomic indicator within this genus. However, we feel that the environmental susceptibility of this character indicates that it may not be a valid measure of species differences.

INTRODUCTION

Two species of the genus *Menidia* (Pisces: Atherinidae) are commonly recognized as occurring in Texas; *Menidia audens*, which is restricted to the Red River Drainage, and *M. beryllina*, which inhabits coastal bays and freshwater impoundments (Hubbs 1972). A recent partial revision of the genus by Johnson (1975) based upon biochemical and morphological characters, reinstates *M. peninsulae* (Goode and Bean) to specific status and reports of its sympatric occurrence in Texas with *M. beryllina.*

Traditionally, the arious species of *Menidia* have been classified by differences in body proportions (Goode and Bean 1879, Kendall 1902, Jordan and Hubbs 1919). In most cases, there are few distinct differences in proportions, rather, most characters vary in a clinal manner. Gosline (1948) reported that the position of the air bladder, with respect to the origin of the anal fin, varied between species of *Menidia* and that this character could be used in evaluating taxonomic relationships.

Johnson (1975) found that in Florida, proportional measurements distinguish *M. beryllina* from *M. peninsulae*, but in Texas, the two species could not be differentiated by external morphological measurements. In Texas populations, according to Johnson, *M. peninsulae* has 3 or fewer anal fin rays ($\bar{x} = 1.56$; $s = 0.75$) in front of the posterior extension of the air bladder, while *M beryllina* has more than 4 anal fin rays ($\bar{x} = 5.1$; $s = 0.74$) in front of the posterior exten-

[1] Order of authors determined by drawing straws.

sion of the air bladder, and the 2 species can be distinguished by this character.

However, useful characters are generally those in which there is little or no correlation between the character and the environment in which the organisms are found. We shall present evidence that the position of the air bladder, with respect to the origin of the anal fin, is influenced by salinity, thus limiting the usefulness of this character in establishing specific relationships and casting doubt upon the reported occurrence of *M. peninsulae* in Texas.

MATERIALS AND METHODS

Specimens were collected by seine at the following Texas localities: Lake L.B.J.; Copano Bay at the Bayside Bridge (location 1); Aransas Bay at Nine Mile Point (location 2); Nine Mile Point Pond (location 3); a brackish-water hurricane basin at Nine Mile Point (location 4); Aransas Bay on the south side of the Aransas Pass Causeway just east of the Intracoastal Canal (location 5) (this site is within 5 km of Johnson's "Laguna Madre" station); Aransas Bay at the Port Aransas Airport on Mustang Island (location 6); dredged pass through Mustang Island at the Intracoastal Canal (G.I.W.W.) (location 7) and the west shore of the Upper Laguna Madre, near Pita Island (location 8). Individuals of *Menidia audens* were collected from Lake Texoma (Fig. 1), adjacent to the University of Oklahoma Biological Station, Oklahoma. Three of the above locations require special mention. Nine Mile Point Pond opened directly into Aransas Bay about 100 m east of this sample site; the adjacent Aransas Bay station was on the other side of a 10 m wide sand bar. The brackish-water basin, located less than 50 m from the Nine Mile Point Pond, is a temporary pond with no connections to other bodies of water, except during storms. This pond has been observed dry (Clark Hubbs pers. comm.) and connected to Nine Mile Point Pond (Hubbs 1962). The fish from this location could be distinguished from all others collected at Nine Mile Point by their greenish coloration, but they must have had their

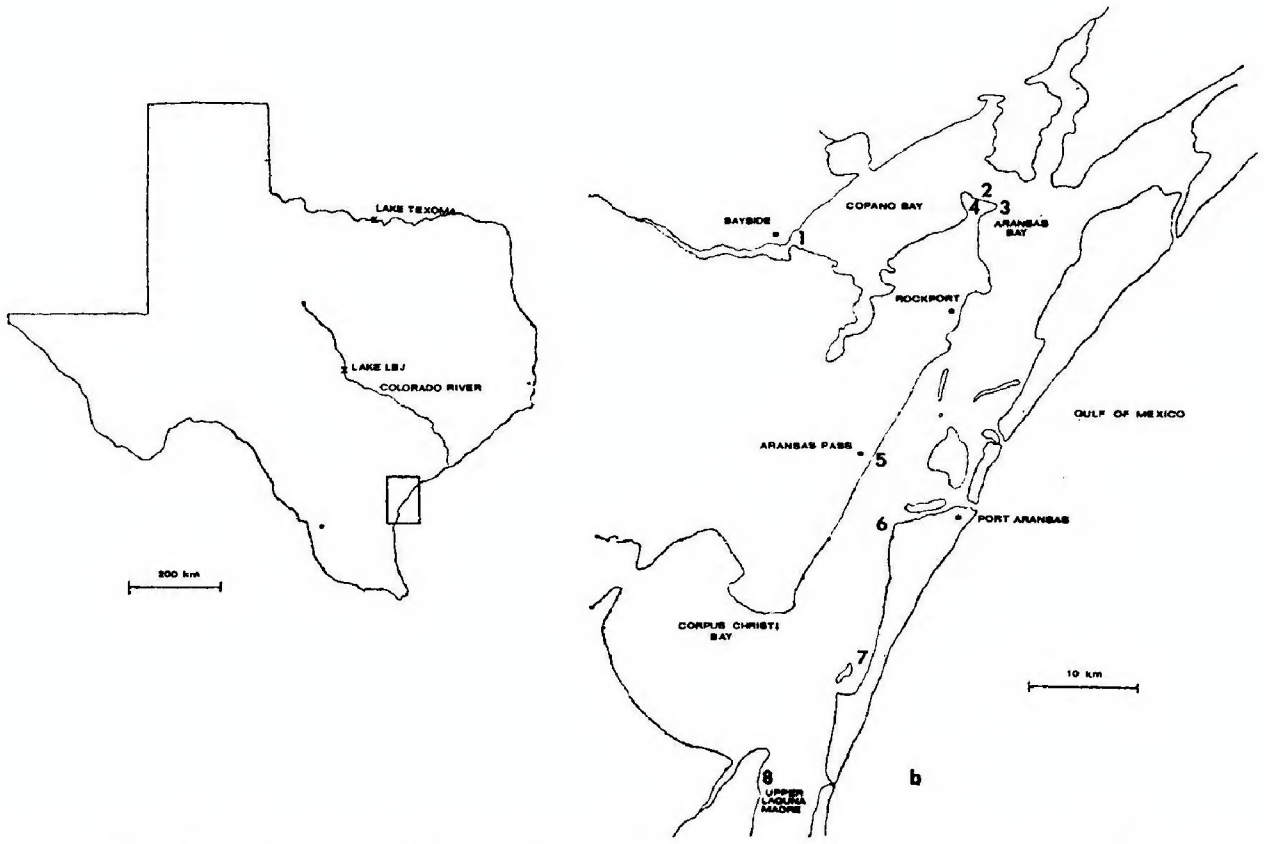

FIG. 1a. Collection locations for *Menidia* in Texas and Oklahoma. Aransas Bay and Upper Laguna Madre sample locations are shown in Figure 1b. Numbers indicate locations referred to in text.

origin from localities 2 or 3. These three locations were less than 0.5 km from Johnson's "Copano Bay" station.

Specimens collected in Texas were preserved in 10% formalin and specimens from Lake Texoma were subdivided into three groups and preserved in 3%, 10% and 40% formalin, respectively, to determine the effect of formalin concentration on the character studied. Temperature and salinity for each location, except Copano Bay, were recorded. Mean salinities for each site were calculated from data collected by Texas Parks and Wildlife personnel from 1969 to 1974.

To determine the number of anal fin rays, including the first spine, beneath the air bladder (hereafter referred to as anal rays), specimens were stained overnight in an alizarin dye, then hemisected, longitudinally, behind the pectoral fin to expose the abdominal cavity. The posterior extension of the air bladder was easily recognized by the adherence of the silvery bladder wall to the surrounding trunk musculature. We noted that the posterior end of the air bladder was not separated from the posterior coelomic wall. Using a straight-edge, a perpendicular was erected tangent to the posteriormost extension of the air bladder and the number of anal rays anterior to his line was counted.

Each specimen was examined by at least 2 of the investigators and any discrepancies, although infrequent, resulted in discarding the specimen. No significant changes in the conclusions occurred by exclusion of those individual counts. The sex and standard length of each specimen were also recorded.

Experimental procedures were conducted at the Port Aransas Marine Laboratory, University of Texas Marine Science Institute at Port Aransas, Texas and at the University of Oklahoma Biological Station, Lake Texoma, Oklahoma. Specimens collected from locations 6 and 7 were returned to the Port Aransas facilities and placed in varying salinities, as indicated in Table 2. The transfer of all specimens into 22 ppt salinity was direct and immediate. The transfer of individuals from locality 7 into 10 ppt and 2 ppt salinities was achieved by dilution over a period of several hours. Individuals alive after 12 hours were preserved in 10% formalin. Live specimens collected from Lake Texoma were returned to the Lake Texoma facilities and placed directly into 40 ppt salt water for 72 hours, after which time, individuals still alive (approximately one-third of the original sample) were preserved in 10% formalin.

Statistical analysis of the data was performed using a CDC 6600 computer and the SPSS statistical program at the University of Texas at Austin.

RESULTS

The frequency distributions of individuals exhibiting various numbers of anal fin rays beneath the posterior extension of the air bladder are shown in Table 1 for all localities. Fishes collected in open bays, where salinities were generally highest, except for the Copano Bay sample, typically had 3 or fewer fin rays beneath the air bladder, whereas those individuals collected from fresh-water impoundments (Lake L.B.J., Lake Texoma) had 5 or more anal rays beneath the air bladder. Those individuals collected from temporary habitats and Copano Bay, however, ranged from 0 to 6 or 7 fin rays under the air bladder.

There is a trend toward lower variation in anal finray number in those samples taken in extreme (either high or low) salinities, while greater variation in anal finray numbers exists in samples from either temporary habitats or from localities with intermediate salinities, indicative of more fluctuating environments. In none of the samples, however, was there a significant bimodal distribution of the number of anal fin rays beneath the air bladder. The number of anal fin rays beneath the air bladder is correlated to both the collected salinity ($r =$

0.57) and to the 5-year mean salinity ($r = 0.62$) of the collection sites. Fin ray number beneath the air bladder (Y) was related to the 5-year mean salinity (X) by the following linear regression equation:

$$Y = (-0.093 \pm 0.006)\, X + (3.678 \pm 0.134)$$

The altered distributions of anal fin ray numbers that resulted from experimental manipulations are shown in Table 2. Those individuals subjected to decreased salinity regimes tended to increase fin ray numbers beneath the air bladder, when compared to preserved specimens from the same locations as shown in Table 1. This increase was of marginal significance for the following samples: G.I.W.W. (26 ppt changed to 22 ppt), $t = 5.44$, $P < 0.05$; G.I.W.W. (26 ppt changed to 10 ppt), $t = 4.03$, $P < 0.05$ and G.I.W.W. (26 ppt changed to 2 ppt), $t = 1.86$, $P < 0.1$. The change in fin ray numbers beneath the air bladder in the Airport sample (28 ppt changed to 22 ppt) was not statistically significant.

Conversely, *M. audens*, when subjected to highly (40 ppt) saline conditions, decreased the numbers of fin rays beneath the air bladder, when compared to previously obtained preserved specimens. The Lake Texoma manipulated sample differed significantly from samples preserved in 3%, 10% and 40% formalin ($t = 3.15$; $t = 4.98$; $t = 4.37$, respectively) at the 0.005 probability level.

Pairwise comparisons of the samples of *M. audens* preserved in different formalin concentrations revealed significant differences in the number of anal fin rays beneath the air bladder between samples preserved in 3% and 10% ($t = 3.59$, $P < 0.01$) and 3% and 40% ($t = 13.82$, $P < 0.001$). Samples preserved in 10% and 40% formalin were not significantly different (Table 2).

TABLE 1

Frequency distribution of anal fin rays (including spine) under the air bladder of Menidia beryllina *from different localities.*

Station	N	0	1	2	3	4	5	6	7	8	9	10	$\bar{X}$	s	Sample Salinity*	5-yr. Mean Salinity*
Lake L.B.J.	75	.	.	.	.	.	7	44	21	2	0	1	6.3	0.78	0	0
Copano Bay	160	4	14	47	41	21	21	13	1	.	.	.	3.1	1.5	-	10.6
Aransas Bay	160	11	82	50	16	1	.	.	.	.	.	.	1.5	0.79	10.3	16.1
Brackish-basin	108	4	10	3	12	19	33	24	2	.	.	.	4.2	1.7	9.9	-
9-Mile Pt. pond	160	12	45	52	22	13	11	5	.	.	.	.	2.2	1.5	10.1	-
Causeway	160	15	73	61	11	.	.	.	.	.	.	.	1.4	0.75	12.0	23.0
Airport	160	27	72	52	8	1	.	.	.	.	.	.	1.3	0.82	28.0	27.2
G.I.W.W.	160	49	87	21	3	.	.	.	.	.	.	.	0.86	0.7	26.0	27.7
Laguna Madre	160	30	90	39	1	.	.	.	.	.	.	.	1.1	0.67	25.9	31.8

* ppt.

TABLE 2

Experimental frequency distribution of anal fin rays (including spine) under the air bladder for selected samples of Menidia.

Sample	Salinity* From	To	N	0	1	2	3	4	5	6	7	8	9	$\bar{X}$	s
Airport	28	22	71	9	32	23	7	.	.	.	.	.	.	1.4	0.84
G.I.W.W.	26	22	53	10	15	17	11	.	.	.	.	.	.	1.6	1.0
G.I.W.W.	26	10	46	13	10	14	9	.	.	.	.	.	.	1.4	1.1
G.I.W.W.	26	2	9	3	2	2	2	.	.	.	.	.	.	1.3	1.2
M. audens	1	40	31	.	.	.	.	1	13	16	1	.	.	5.6	0.62
M. audens	(3% formalin)		70	.	.	.	.	.	15	41	13	1	.	6.0	0.68
M. audens	(10% formalin)		20	.	.	.	.	.	1	10	4	4	1	6.7	1.0
M. audens	(40% formalin)		70	.	.	.	.	.	12	30	23	4	1	6.3	0.88

* ppt.

DISCUSSION

The recent suggestion by Johnson (1975) that there are two species of *Menidia* (*beryllina* and *peninsulae*) occurring sympatrically in Texas coastal waters is based upon his observations of differences in 5 electrophoretically determined loci among populations from different localities and of differences in the posterior extension of the air bladder as measured by the number of anal rays plus the anal spine observed beneath it. In areas where *M. beryllina* and *M. peninsulae* were considered to be sympatric (i.e. brackish-water areas), Johnson noted a bimodal distribution of anal ray numbers beneath the air bladder.

In this study we have investigated the morphological character which Johnson claims can be used to distinguish the 2 species and we have found several lines of evidence which suggest that this character is unsound for this purpose. The number of anal fin rays beneath the air bladder varies clinally with salinity. The clinal nature of this attribute is demonstrated by the data obtained from the G.I.W.W. station. That average is extreme for those listed by Johnson for *M. peninsulae*. Furthermore, that station is the least likely to have freshwater impact of any studied by us. Similarly, the Lake L.B.J. sample represents extreme *M. beryllina* in this character in comparison with Johnson's samples. Moreover, the distribution of anal rays beneath the air bladder is unimodal at all but one sample location, including most brackish-water locations in which the total variation in fin ray number beneath the air bladder is greatest. The slight bimodality noted in the brackish-basin samples does not correspond to Johnson's criterion for the separation of *M. peninsulae* and *M. beryllina*. If anything, the distribution we obtained would suggest a bimodality of fin ray numbers within what Johnson would consider *M. peninsulae*.

There are also significant differences between most sample locations even when the maximum number of anal fin rays beneath the air bladder, in each

location, fell within the limits of what Johnson would call a single species. For example, the Airport sample differed from the G.I.W.W. sample ($t = 4.81$; $P < 0.001$) and the Aransas Bay sample ($t = 2.05$; $P < 0.05$), within the same bay system.

The number of anal fin rays beneath the air bladder was significantly different ($t = 10.1$; $P < 0.05$) between populations at Nine Mile Point pond and the brackish-water basin, and these populations differed significantly from the nearby Aransas Bay population ($t = 5.6$ and 17.3, respectively; $P < 0.05$). These differences, as well as differences in coloration (open bay fish are silvery and temporary pond fish are greenish), must be attributed to differences in the habitats, including salinity differences, since the Aransas Bay population repeatedly has resupplied the temporary pond population when the pond refills, after drying, during periods of storm-related high water.

The direction of the variation in anal fin ray number beneath the air bladder corresponds to that predicted by the function of the air bladder itself. In pelagic species, the air bladder is primarily a bouyancy organ, and to function efficiently as such it must have the capacity to respond to changes in the specific gravity of the fish relative to that of the water. Individuals moving from saline conditions into somewhat fresher water would be expected to increase the size of the air bladder (and hence the number of anal rays observed beneath it) to compensate for the lowered specific gravity of the water. Conversely, individuals moving into more saline conditions should show a decrease in air bladder size. Black (1948) demonstrated that the volume of gases removed from the air bladder of *Fundulus heteroclitus* is dependent upon the salinity in which the fish is maintained, and that the volume was greatest in fresh water and decreased with increasing salinity. Our experimental results also indicate that the size of the air bladder is dependent upon the salinity of the medium. In all samples introduced into lowered salinities, with the exception of the Airport sample, the mean number of anal rays beneath the air bladder increased significantly. The Airport sample also showed increased numbers of anal rays beneath the air bladder, but the difference from the control population was not significant. We believe that the temperature shock associated with this introduction may have affected this result. The sample from the G.I.W.W. which was introduced into 2 ppt salinity exhibited a change from the control population that was significant only at the 90% level. The small sample size ($N = 9$), in this case may be responsible for this result. It is, however, possible that these individuals experienced a rapid chloride depletion upon introduction to such a vastly different salinity such as was reported by Black for *F. heteroclitus*. Chloride is known to be involved in the air bladder filling mechanism of fishes; hence, massive chloride losses would presumably decrease the rate of filling of the air bladder.

The differences in the number of anal fin rays beneath the air bladder between the samples preserved in different formalin concentrations, do not follow any apparent trend, but it is clear that the concentration of the preservative does have an effect on this character. Individuals placed in 10% and 40% formalin die almost immediately and it may be that the mean number of anal fin rays

observed beneath the air bladder in these samples is that which would be found in non-preserved, freshly killed specimens. If this is the case, then the significant decrease observed in the sample preserved in 3% formalin may be a response to increased osmolarity (relative to fresh water) coupled with an increased response time, because the time until death in 3% formalin is noticeably longer than at higher concentrations.

From the data gathered and for the reasons stated above, we feel that the posterior extension of the air bladder in *Menidia beryllina* is an environmently susceptible character and that its use as a taxonomic indicator is unjustified. Further, principal coordinate projection analysis by Mickevich and Johnson (1976), showed that allozyme differences between *M. beryllina* and *M. peninsulae* are separable only upon the secondary axis, not the primary axis, whereas their morphometric results did not differentiate the two groups on either the primary or the secondary axis. On these grounds, we reject the Johnson hypothesis that *M. peninsulae* co-exists with *M. beryllina* in Texas waters.

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We are indebted to Dr. Clark Hubbs for generously giving his time, assistance and ideas throughout the course of this study. David Wilhite, Thomas Lucier and Kee Srithavatzh kindly assisted in the collection of specimens. We wish to thank the staff of the Port Aransas Marine Laboratory, University of Texas Marine Science Institute at Port Aransas for providing laboratory space and for other considerations.

LITERATURE CITED

BLACK, VIRGINIA S. 1948 Changes in density, weight, chloride, and swim-bladder gas in the killifish, *Fundulus heteroclitus*, in fresh water and sea water. *Biol. Bull.* **95**:83–93.

GOODE, G. B. and T. B. BEAN. 1879. Catalogue of a collection of fishes sent from Pensacola, Florida, and vicinity, by Mr. Silas Stearns, with descriptions of six new species. *Proc. U.S. nat. Mus.* **2**:121–156.

GOSLINE, W. A. 1948. Speciation in the fishes of the genus *Menidia*. *Evolution.* **2**:306–313.

HUBBS, Clark. 1962. Effects of a hurricane on the fish fauna of a coastal pool and drainage ditch. *Tex J. Sci.* **14(3)**:289–296.

————. 1972. A checklist of Texas freshwater fishes. *Tech. Ser. Tex Parks Wildl. Dept.*, No. **11**: 11 pp.

JOHNSON, MICHAEL S. 1975. Biochemical systematics of the atherinid genus. *Menidia. Copeia.* **1975(4)**:662–691.

JORDAN, D. S. and C. L. HUBBS. 1919. Studies in ichthyology: A monographic review of the family Atherinidae or silversides. *Stanford Univ. Pubs.* Univ. Ser. 87, pp., 12 plates.

KENDALL, W. C. 1902. Notes on the silversides of the genus *Menidia* of the east coast of the United States, with descriptions of two new subspecies. *Rept. U.S. Comm. Fish and Fisheries for* **1901**:241–267.

MICKEVICH, M. F. and MICHAEL S. JOHNSON. 1976. Congruence between morphological and allozyme data in evolutionary inference and character evolution. *Syst. Zool.* **25**:260–270.

TEXAS PARKS AND WILDLIFE DEPT. 1969–1974. *Coastal Fisheries Project Reports.*

SPECIES COMPOSITION AND SEASONAL PERIODICITY OF THE MARINE BENTHIC ALGAE OF GALVESTON ISLAND, TEXAS

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Sampling of benthic algae from selected sites on Galveston Island was carried out at regular intervals between June 1972 and August 1974 to determine the species composition and seasonal periodicity of the communities. Nineteen genera and twenty eight species were recorded; 8 species of Chlorophyta, 5 Phaeophyta, 14 Rhodophyta and 1 Xanthophyta. The ocean-front benthic algal community of the island is described as a *Cladophora-Bryocladia-Ceramium* community in the summer which shifts to an *Enteromorpha-Bangia-Gelidium* community in the winter months. The bay stations are described as an *Enteromorpha-Ectocarpus* community in the winter months and are essentially barren of benthic algae in the summer. Results of the study regarding species composition are compared to similar Gulf coast studies.

INTRODUCTION

Relatively little has been reported regarding the benthic algae of the upper western Gulf Coast. W. R. Taylor (1954) summarized the information known at that time about the algae from the Gulf of Mexico. He suggested that the Gulf Coast flora consisted primarily of tropical forms with a few temperate and widespread species. Humm and Hildebrand (1962) published a survey of the algae of the southern Gulf of Mexico from Rockport, Texas, to the Yucatan Peninsula of Mexico. Humm (1956, 1963), Humm and Caylor (1957), Humm and Darnell (1959), and Humm and S. Taylor (1961) published extensive taxonomic and distribution studies dealing with the marine algae of Florida and the eastern Gulf Coast. Conover (1964) contributed a fourteen month survey of the algae of the Texas lagoons from Corpus Christi southward to Port Isabel. Conover (1958) also compared these data to data from a lagoon in New England coastal waters. Earle (1969) presented a study of the Phaeophyta of the eastern Gulf of Mexico including the coastline and adjacent continental shelf from the Mississippi Delta at Barataria Pass to the Dry Tortugas, Florida. Earle (1972) compiled and analyzed data obtainable at that time and presented a general plan of the nature of the algae of the entire Gulf Coast. Dawes and Van Breedveld (1969) compiled the results of monthly collections from an extensive 28 month ecological survey of the continental shelf of Florida between the entrance to Tampa Bay and Fort Myers at depths of 6 to 73 meters. The results of these collections support the opinions of others (Humm and S. Taylor 1961, Earle 1969) that

there is a rich benthic algal flora of perennial and annual, subtropical (warm temperate) and tropical species on the inner continental shelf along the Florida Gulf Coast supplemented during the winter months with seasonal cold temperate species. The large number of perennial plants found in depths of 20 to 60 meters agreed with the apparently stable temperature, salinity, and light penetration at the deeper stations. In contrast, the shallow water stations of these studies indicated a more sparse flora with pronounced seasonality. This was explained by the lack of a suitable substrate coupled with the wide range in temperature and salinity during the year. A second general feature of these collections was the predominance of tropical species, especially in the 20 to 80 meter depths. Dawes' book (1947), Marine Algae of the West Coast of Florida, with line drawings and keys, has synthesized much scattered information concerning benthic algae of the west coast of Florida. Edwards' (1969, 1970) and Edwards and Kapraun's (1973) studies, although limited to the area of Port Aransas, Texas, are among the most thorough for any part of the Gulf of Mexico. Data regarding species abundance, phytogeography, periodicity, sexuality, and morphology were recorded. A vegetative key was formulated and the work included photographs of each species found in the area. Edwards (1970) also presented a literature survey of the existing field studies comparing seasonal changes in algal vegetation and environmental factors. Kapraun (1970) published material specific to the marine Chlorophyta of the Port Aransas area. Kaupraun (1974) also completed an extensive study dealing with periodicity and phytogeography of benthic marine algae in Louisiana. Offshore collections were made in addition to well-spaced sites along the coast. Keatts (1969, unpublished) surveyed the algae on a rock jetty in Freeport, Texas, over a 12 month period and Sorensen (1972, unpublished) has kept records of the occurrence of the benthic algal flora at South Padre Island. No extensive information has been reported concerning benthic marine algae of the Galveston, Texas, area.

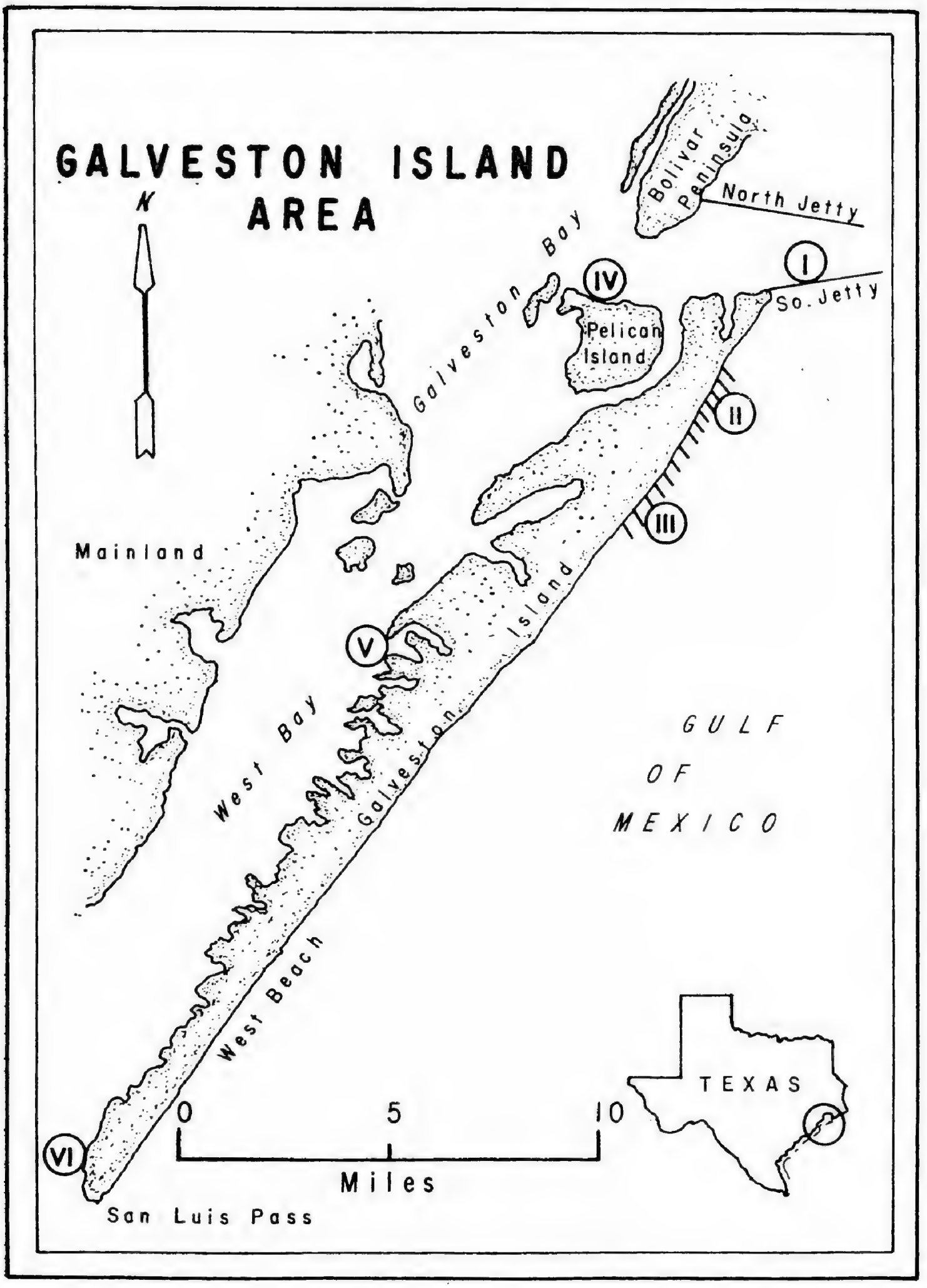
MATERIAL AND METHODS

Description of Study Area

Galveston Island (Fig. 1) is situated approximately 40 miles S.E. of Houston, Texas, and is a portion of the series of barrier islands extending along the length of the Texas and Louisiana coasts. The island is 25 miles long and ranges from approximately 0.7 to 3 miles wide. The city and port of Galveston lie at the eastern end of the island and this area is guarded by a concrete sea wall and a series of short granitic rock jetties projecting from the sea wall.

The island is typical of the barrier islands in having little natural structure suitable for abundant algal growth. The beaches consist of fine, well-washed sand with rocks or reefs essentially absent. However, the extensive series of artificial rock jetties, piers, and other man-made projections and rubble from the Galveston sea wall afford ample structure for the establishment of introduced species of algae if such species can tolerate the climate and water quality.

The climatic conditions fluctuate widely, a situation which is typical of the northern Gulf Coast. Changes in both temperature and salinity can occur rapidly during the year. In 1972, in Galveston, the average daily maximum temperature was 24.3°C and the average daily minimum 18.8°C. The 1972 annual average temperature was 21.6°C and extremes ranged from —1.7°C on 5 January to 33.9°C on 27 August. Galveston Island is adjacent to the largest estuarine system on the Texas coast and, thus, salinities fluctuate often and rapidly with rainfall.


GALVESTON ISLAND AREA
N
Bolivar Peninsula
North Jetty
Galveston Bay
IV
I
So. Jetty
Pelican Island
II
III
Mainland
Island
V
West Bay
Galveston
GULF OF MEXICO
West Beach
TEXAS
VI
0
5
10
Miles
San Luis Pass

Collection Stations

Collecting station locations are illustrated in Fig. 1.

Station I was the South Jetty, one of the two jetties guarding the channel which separates Galveston from Bolivar and is the mouth of the Houston ship channel. Both of these jetties are approximately 1.5 miles long with water on both sides of the east 0.5–0.9 miles of the jetties. The structures are trapezoidal in cross section; about 10 feet wide at the apex and about 2 miles apart. The South Jetty, due to its size and location, proved to be the most important station.

Station II was a county fishing groin located near the eastern end of the island projecting from the sea wall at 17th street. The structure is approximately 75 yards long and T-shaped, affording several areas protected from heavy wave action.

Station III was a granitic groin, projecting from the sea wall at 50th street. The structure is approximately 75 yards long and 9 feet wide at its apex. This straight type is the most common projection from the Galveston sea wall.

Station IV was the old quarantine station, now a county park, located at the tip of Pelican Island. This station has strategic location on the bay, adjacent to the channel. It is surrounded with large granite boulders of the same type used in the construction of the jetties.

Station V was typical of the bay side of Galveston Island, an extensive *Spartina* marsh bordering a wide shallow bay. Substrate at this station was confined to the *Spartina*, rocks, oyster beds, wooden pilings, and piers.

Station VI was a fishing camp located adjacent to San Luis Pass at the extreme west end of the island. This station was also essentially a salt marsh.

Collecting Procedures

Stations were sampled monthly to bi-monthly from June 1972 to June 1973 and were studied intensively for a seven week period June 1973 to August 1973. Irregular collecting trips were made during the fall of 1973.

Specimens were examined microscopically to identify the species, to locate epiphytes, and to identify sexual stages of the algae. In most cases, the species were determined using the criteria established by Edwards (1970).

RESULTS

Species Composition

The following is an annotated list of the benthic eucaryotic algae collected and identified during this study. Table 1 presents the results of the study by month and collecting station, showing the locale and seasonal distribution of the species collected. Terms relating to zonation are the same as those used by Edwards (1970). Cyanophyta were also encountered throughout the investigation on the jetties and mudflats. These were predominantly of the order Oscillatoriales.

Chlorophyta

Enteromorpha clathrata (Roth) Greville

Occurs throughout the year in the eulittorial zones of ocean front groins. Found in limited amounts at the bay stations during the winter months. Reaches maximum growth in late winter and early spring when it is obviously the dominant species on the island. Scarce at all stations in October and November.

E. flexuosa (Wulfen ex Roth) J. Agardh

Relatively abundant on the channel side of the South Jetty and at the Quar-

TABLE 1

Presence of Algae at Galveston Island Collecting Stations During the Investigation

Table I. Presence of Algae at Galveston Island Collecting Stations During the Investigation

	Study Collections	1972						1973							
	Stations[1]	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul
CHLOROPHYTA															
Enteromorpha clathrata	I II III	x[2]	x	x	x	x	x	*	*	*	*	*	*	*	x
	IV	-	nc	nc	nc	-	x	x	x	x	x	nc	nc	nc	nc
	V VI	-	-	-	-	-	x	x	x	x	x	x	x	-	-
E. flexuosa	I II III	-	-	-	-	-	-	-	x	x	-	-	-	-	-
	IV	-	nc	nc	nc	-	-	x	x	*	*	nc	nc	nc	nc
	V VI	-	-	-	-	-	-	-	*	*	-	-	-	-	-
E. lingulata	I II III	x	x	x	x	x	x	x	x	*	*	*	*	x	x
	IV	-	nc	nc	nc	x	x	x	x	x	x	nc	nc	nc	nc
E. prolifera	I II III	-	-	-	-	-	-	?	?	?	-	-	-	-	-
	IV	-	nc	nc	nc	-	-	*	*	*	*	nc	nc	nc	nc
	V VI	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ulva lactuca	IV	-	nc	nc	nc	-	-	x	x	x	-	nc	nc	nc	nc
	V VI	-	-	-	-	-	x	x	*	*	x	-	-	-	-
Chaetomorpha linum	I II III	x	x	x	*	*	*	x	-	-	-	x	-	x	x
Cladophora dalmatica	I II III	x	x	*	*	*	*	x	x	x	x	x	x	x	x
C. delicatula	I II III	x	-	x	*	-	x	-	-	-	-	-	-	-	x
PHAEOPHYTA															
Ectocarpus siliculosus	I	-	-	-	-	-	-	-	x	x	-	-	-	-	-
	IV	-	nc	nc	-	-	nc	x	x	x	x	nc	nc	nc	nc
	V VI	-	-	-	-	-	x	*	*	*	x	-	-	-	-
Dictyota dichotoma	V	-	-	-	-	x	-	-	-	-	-	-	-	-	-
Petalonia fascia	I	-	-	-	-	-	-	-	x	-	-	-	-	-	-
	IV	-	nc	nc	-	-	nc	x	*	*	-	-	-	-	-
RHODOPHYTA															
Goniotrichum alsidii	I II III	-	-	x	-	x	-	-	-	-	-	-	-	-	-
Erythrocladia subintegra	I II III	x	-	x	x	x	x	-	x	-	-	x	x	x	x
	IV	-	nc	nc	-	x	nc	nc	-	-	-	nc	nc	nc	nc
Erythrotrichia carnea	I II III	x	x	x	x	x	x	x	x	-	-	-	x	x	x
	IV	-	nc	nc	x	x	nc	nc	-	-	-	nc	nc	nc	nc
Bangia fuscopurpurea	I II III	-	x	-	-	-	-	x	x	*	*	x	-	-	-
	IV	x	nc	nc	-	-	nc	nc	x	x	*	nc	nc	nc	nc
Acrochaetium spp.	I II III	-	-	x	x	x	-	x	x	x	-	x	x	x	x
	V VI	-	-	x	x	x	-	-	-	-	-	-	x	*	*
Gelidium crinale	I II III	-	x	-	-	x	x	x	x	*	*	*	*	*	x
Gracilaria foliifera	VI	-	-	-	-	x	-	-	-	-	-	-	-	-	-
Ceramium strictum	I II III	x	x	*	*	*	x	x	-	-	-	-	-	-	x
	IV	x	nc	nc	nc	x	x	x	-	-	-	nc	nc	nc	nc
Spyridia filamentosa	VI	-	-	-	-	x	-	-	-	-	-	-	-	-	-
Polysiphonia denudata	I II III	-	-	-	-	x	x	x	x	x	-	-	-	-	x
P. subtilissima	V	-	-	-	x	-	-	-	-	-	-	-	-	-	-
P. tepida	I II	-	-	-	x	-	-	-	-	-	-	-	-	-	-
P. gorgoniae	VI	-	-	-	-	x	x	-	-	-	-	-	-	-	-
Bryocladia cuspidata	I II III	x	x	*	*	*	*	x	-	-	-	-	-	x	x
	IV	x	nc	nc	nc	-	-	-	-	-	-	-	nc	nc	nc

1. STATION KEY
   - I - South Jetty
   - II & III - Ocean Front Groynes
   - IV - Quarantine Station
   - V & VI - Bay Stations

2. x - Present
   - * - Maximum
   - - - Not Present
   - nc - No Collection Made
   - ? - Probable.

antine Station on Pelican Island in January and February. Absent in summer months.

E. prolifera (Mueller) J. Agardh

Occurs from the Quarantine Station on Pelican Island during the winter; abundant in February. Typical morphology is exhibited only in relatively calm water. Absent in summer months.

E. lingulata J. Agardh

Occurs throughout the year on the ocean front jetties and on the South Jetty and at the Quarantine Station in the winter months. Reaches maximum development in the late spring.

Ulva lactuca Linnaeus

Occurs during the winter and early spring from the bay stations and from the protected water adjacent to the Quarantine Station on Pelican Island. Usually attached to rock rubble. Common but never abundant. It never reached the maximum size reported by Edwards (1970). Absent during the summer months.

Chaetomorpha linum (Mueller) Kuetzing

Lives in depressions on the top of the South Jetty and rock jetties ffrom March to December. Most frequent in summer months. Edwards (1970) reports a morphological variety of this species found in quiet bay waters of the Port Aransas area. This form was not encountered at Galveston.

Cladophora dalmatica Kuetzing

The extremely polymorphic genus made many determinations indecisive. Most specimens collected agree well with Edwards' description of *C. dalmatica.* Very abundant in late summer in the eulittoral zone on the ocean side of the South Jetty and to a lesser extent on small jetties. Less common in winter. It was absent from February collections.

Cladophora delicatula Montagne

Indecisive determinations. Most specimens collected agree well with Edwards' description of *C. delicatula.* Uncommon and sporadic in warmer months from ocean front groins.

Phaeophyta

Ectocarpus siliculosus (Dillwyn) Lyngbye

Collected from bay stations from mid-November to March. Uncommon at ocean front stations. Most specimens were found in calm water. Absent from summer collections.

Dictyota dichotoma (Hudson) Lamouroux

Collected once in October, 1972, from the grassbeds adjacent to a San Luis Pass fishing camp. May be common in other years.

Petalonia fascia (O. F. Mueller) Kuntze

Collected in the winter of 1972–73 from the old Quarantine Station on Pelican Island in the eulittoral zone of the large quarry rocks surrounding the island. Collected rarely from protected areas along the South Jetty. Absent during summer months. Not collected during the winter of 1973–74.

Sargassum fluitans Boergesen

Drift, occurs sporadically throughout the year.

S. natans (Linnaeus) J. Meyen

Drift, occurs sporadically throughout the year.

Rhodophyta

Goniotrichum alsidii (Zanardini) Howe

Grows as an epiphyte on large algae (predominantly *Cladophora* spp. and *Chaetomorpha linum*) during the summer and fall months. Not collected from bay stations. Uncommon.

Erythrotrichia carnea (Dillwyn) J. Agardh

Grows as an epiphyte on larger algae (predominantly *Cladophora spp.*, *Chaetomorpha linum*, and *Bryocladia cuspidata*) during the summer and fall months. Not collected from bay stations. Common.

Erythrocladia subintegra Rosenvinge

Grows as an epiphyte on larger algae (predominantly *Cladophora* spp. and *Chaetomorpha linum*) during the summer and fall months. Not collected from bay stations. Common.

Bangia fuscopurpurea (Dillwyn) Lyngbye

Grows on the littoral fringe of the South Jetty and jetties in winter and early spring. Very infrequent to absent in summer collections.

Acrochaetium spp.

Indecisive determinations. Most specimens collected agree well with descriptions of *A. flexuosum*. Probably present throughout the year, but collected only during warmer months. Epiphytic on larger algae (*Cladophora* spp., *Bryocladia cuspidata*) and sea grasses (*Thalassia*) at all stations. Most abundant at bay stations.

Gelidium crinale (Turner) Lamouroux

Occurs throughout the year from the eulittoral zones of ocean front stations, most abundant from November to April. This species was rare during the summer of 1972, but was relatively common during the summer of 1973.

Gracilaria foliifera (Forsskål) Boergesen

Collected once in October 1972 from grassbeds adjacent to a fishing camp near San Luis Pass. May be common other years.

Spyridia filamentosa (Wulfen) Harvey

Collected once in October 1972 from grassbeds adjacent to a San Luis Pass fishing camp.

Ceramium strictum (Kuetzing) Harvey

Collected from June to mid-November in the eulittoral zones of the South Jetty and smaller rock jetties. Maximum growth was in late summer and early fall when it was one of the dominant forms on the ocean front stations.

Polysiphonia denudata (Dillwyn) Kuetzing

Collected from the sublittoral zone of the South Jetty, usually attached to oyster shells, during the fall and winter of 1972. Collected from the tips of the smaller jetties during the summer of 1973.

Polysiphonia subtillissima Montagne

Collected in the fall of 1973 from a salt marsh at Sportsman Road. Attached to *Spartina* sp. Uncommon.

Polysiphonia tepida Hollenberg

Collected from September to February, 1973 in the protected eulittoral zones of the South Jetty and from the 17th street fishing pier. This alga was not collected in 1972. Was a dominant alga in the fall of 1974 on the South Jetty.

Polysiphonia gorgoniae Harvey

Occurs as an epiphyte on *Halodule wrightii* from the bay station at San Luis Pass in the fall of 1972. Uncommon.

Bryocladia cuspidata (J. Agardh) De Toni

Occurs from the eulittoral zones of all ocean front stations from June through December. Reaches maximum development in late summer and fall when it is the dominant alga on the ocean front structures. Most abundant in areas of heavy wave action.

Xanthophyta

Vaucheria sp.

Collected floating in tangled mats from a shallow bay at the end of six-mile road in the fall of 1972. A brackish water species. Common.

Observations Concerning Periodicity of the Flora

This investigation revealed 19 genera and 28 species of benthic marine algae in the area of Galveston Island, excluding Cyanophyta. The two species of *Sargassum* are pelagic forms which sporadically wash ashore along the length of

the Gulf coast. Three species, *Gracilaria foliifera*, *Dictyota dichotoma*, and *Spyridia filamentosa* were collected as drifts on one occasion and, then, only plant fragments were present. A close approximation of the Island's standing algal flora appears to be 16 genera and 25 species. Keatts (1969, unpublished) reported 14 genera and 20 species from a granite jetty at Freeport, Texas.

Most of the 28 species of benthic marine algae exhibited pronounced seasonality. The maximum growth periods as observed in this study are presented in Table 2.

The summer flora of 1972 consisted predominantly of *Enteromorpha clathrata*, *Cladophora* sp., *Bryocladia cuspidata* and *Ceramium strictum*. Growth was limited to the South Jetty, the smaller jetties and rubble associated with the Galveston sea wall. The littoral fringe or upper intertidal zone was dominated by *Enteromorpha clathrata*, *E. lingulata* and *Cladophora* spp. *Cladophora* spp. were more pronounced on the South Jetty, reaching maximum development in August. The eulittoral zone was dominated by *Bryocladia cuspidata* and *Ceramium strictum*. As the summer progressed the proportions of species of *Enteromorpha* decreased as *Bryocladia cuspidata* and *Ceramium strictum* increased.

The bay stations in the summer of 1972 had virtually no benthic algae except for mats of filamentous Cyanophyta of the *Oscillatoria* type. A bloom of *Spyridia filamentosa* (Rhodophyta) was observed in early June 1972, from the grassbeds adjacent to San Luis Pass. This species was not encountered in the spring or summer of 1973. *Acrochaetium* spp. were found as summer epiphytes on *Thallasia testudinum* and *Halodule wrightii*.

The flora of the quarantine station of Pelican Island in summer 1972 consisted essentially of a sparse growth of *Bryocladia cuspidata* and *Ceramium strictum*. Scant patches of *Enteromorpha* (*E. lingulata*) were present. In mid-July of 1972 the granite rocks at the end of the island were covered with a thick tar-like substance that destroyed the algal community until September when tufts of *Ceramium strictum* and *Enteromorpha* spp. became evident. *Bryocladia cuspidata* did not reestablish at this station that year.

TABLE 2

Maximum growth periods of species of benthic algae of Galveston Island (1973–1974).

Summer-Fall Maximum	Winter-Spring Maximum
Bryocladia cuspidata	*Ectocarpus siliculosus*
Ceramium strictum	*Petalonia fascia*
Cladophora spp.	*Entermorpha clathrata*
Polysiphonia gorgoniae	*E. prolifera*
Polysiphonia denudata	*E. flexuosa*
Polysiphonia tepida	*Ulva lactuca*
Spyridia filamentosa	*Gelidium crinale*
Chaetomorpha linum	*Bangia fuscopurpurea*
Erythrocladia subintegra	*Polysiphonia subtilissima*
Erythrotrichia carnea	
Goniotrichum alsidii	
Achrochaetium sp.	

Bryocladia cuspidata and *Ceramium strictum* reached maximum development on all ocean front stations in October, 1972; these two species were dominant. *Cladophora* spp. also reached maximum development in October of both 1972 and 1973. These algae covered the upper eulittoral zone just above the rhodophyte community. *Cladophora* spp. became less abundant as one progressed seaward along the south jetty. *Enteromorpha clathrata* still occupied a narrow littoral fringe zone on the South Jetty, but was much reduced in October from the smaller structures. The rocks of the Quarantine Station in October, 1972 were populated predominantly with *Ceramium strictum* and intermingled tufts of *Enteromorpha* sp.

Late November, 1972 was a period of noticeable, dramatic change in the island's algal community. *Ceramium strictum*, a dominant alga in October and November, was found by mid-December on all ocean front collecting stations only after thorough investigations.

The positions occupied by this species, usually on the protected eulittoral zones of the jetties, were taken by *Gelidum crinale*, which was an uncommon alga during the summer and fall of 1972. *Bryocladia cuspidata* also declined dramatically in abundance, especially on the smaller piers and fishing jetties where it occurred only in isolated patches in mid-winter. The alga was present predominantly in the form of dead thalli on the tips of the groins and on the west side of the South Jetty. Apparently healthy populations of *Bryocladia cuspidata* were evident later in the year (January) on the South Jetty than on the smaller structures.

Species of *Enteromorpha*, predominantly *E. clathrata*, dominated all ocean front stations and available substrate during the winter and spring of 1972–73. *Enteromorpha* spp. began increasing in abundance during November and December. In late February the surface of the South Jetty was covered by a thick carpet of this species. *Bangia fuscopurpurea* and *Gelidium crinale* were the primary species that complemented the winter-spring floral climax with *Enteromorpha* spp.

Benthic algal growth in the bay stations became luxuriant in late November of 1972 and 1973. At this time tufts of *Enteromorpha* spp. and *Ectocarpus siliculosus* were noticed and within a month were covering the available substrate. To a much lesser extent, *Ulva lactuca* and *Polysiphonia subtilissima*, were a part of the bay's winter algal population and reached maximum growth in February and early March.

January and February was the period of most extensive algal development on the rocks of the Quarantine Station in the winter of 1972–73. At this time *Enteromorpha* spp. dominated growth on the well-washed portions with *Petalonia fascia* and *Bangia fuscopurpurea* also evident. The calmer areas of this station were populated predominantly with *Ectocarpus siliculosus* and *Enteromorpha prolifera*.

There was a period, May through June, when the greater part of the winter flora was stagnant and summer forms had not appeared. During this time growth

was essentially limited to the jetties and was dominated by *E. clathrata* and *Bangia fuscopurpurea.*

The benthic algal population of Galveston, with regard to species and abundancies of species, is likely to be relatively inconsistent from year to year, reflecting the environment. *Ceramium strictum*, a dominant form on the jetties by July, 1972 did not appear in noticeable proportions until August, 1973. *Polysiphonia denudata* was abundant on the tips of the short jetties in the littoral zone during the summer of 1973. This alga was not collected in the summer of 1972, either because it was absent or so scare that it was overlooked. A similar case was found with *P. tepida.* The alga was not collected in 1972, but was relatively common from protected areas of the South Jetty in the fall of 1973, and even more noticeable in the fall of 1974. *Gelidium crinale* was scare in the summer of 1972, but was a dominant part of the benthic algal community in July of 1973. From all indications, *Petalonia fascia* failed to reappear in the winter of 1973–74.

Further evidence of the unstable nature of the Galveston algal flora could be the isolated occurrence of *Gracilaria foliifera*, *Spyridia filamentosa*, and *Dictyota dichotoma.* These forms may be present in minute proportions or absent except for years when the proper conditions are present for their establishment. This is especially probable for the bay forms.

DISCUSSION

Results of this investigation indicate that the benthic algal flora of Galveston Island, is sparse, when compared to the flora of other coastal areas in the Gulf of Mexico.

Similar coastal studies by Edwards and Kapraun (1973) in South Texas and Kapraun (1974) in Louisiana, indicate that a reduction in tropical algal species occurs as one progresses north along the Gulf coast from Florida or from Yucatan. There is a dramatic reduction in the number of species of benthic marine algae from the Port Aransas area to Galveston. Edwards reported approximately 91 species representing 57 genera from the Port Aransas area, roughly three times more than were encountered in the Galveston area investigation.

The greater diversity and abundance of algae in the Port Aransas area is very evident, especially with the Rhodophyta. Three species, *Bryocladia cuspidata*, *Ceramium strictum*, and *Gelidium crinale* are essentially the only species of rhodophytes that have well developed populations in Galveston. *Polysiphonia* spp. were found sporadically and were never abundant from any station. This situation is dramatically different from the flowing gardens of *Rhodymenia*, *Hypnea*, *Centroceras*, *Bryocladia*, *Ceramium*, *Porphyra* and other rhodophytes visibly evident on the southwest jetty of Port Aransas. The bays of the Port Aransas areas are also populated with healthy communities of *Gracilaria*, *Spyridia*, *Solieria*, *Digenia*, *Chondria* and others. In the Galveston bay stations, benthic algal growth was found to be limited to winter populations of *Ectocarpus* and *Enteromorpha* with a rare isolated rhodophyte.

Kapraun (1974) encountered thirty species of benthic algae in monthly field

TABLE 3

Comparative Benthic Algal Studies Along the Gulf Coast
(X = present; ? = probably present)

	Port Aransas	Freeport	Galveston	Louisiana
	Edwards 1970	Keatts 1969	Lowe and Cox 1978	Kapraum 1974
CHLOROPHYTA				
Class Chlorophyceae				
Order Ulotrichales				
Ulothrix flacca	X			X
***Entocladia viridis*	X			
E. testarum	X			X
Ulvella lens	X	X		
Order Ulvales				
Blidingia marginata				X
B. minima				X
Enteromorpha clathrata	X		X	X
E. flexuosa	X		X	X
E. lingulata	X		X	X
E. prolifera	X		X	
E. ramulosa	X			X
E. salina	X			X
E. linza	X			X
Ulva fasciata	X			
U. lactuca	X		X	X
Pseudoclonium submarinum				?
Order Cladophorales				
Chaetomorpha linum	X	X	X	X
Cladophora albida	X			
C. dalmatica	X		X	X
C. delicatula	X		X	
C. ruchingeri	X			
C. vagabunda	X			
C. repens				X.
Order Codiales				
Derbesia vaucheriaeformis	X			
Bryopsis hypnoides	X			
B. plumosa	X			
Order Dasycladales				
Acetabularia crenulata	X			
PHAEOPHYTA				
Class Phaeophyceae				
Order Ectocarpales				
Bachelotia antilarum				X
Ectocarpus siliculosus	X		X	X
Giffordia indica	X			
G. mitchelliae	X			X
G. rallsiae	X			X
Streblonema oligosporum	X			X
Streblonema sp.	X			

TABLE 3 (Continued)

	Port Aransas	Freeport	Galveston	Louisiana
	Edwards 1970	Keatts 1969	Lowe and Cox 1978	Kapraum 1974
Order Dictyotales				
Dictyota dichotoma	x		x	
Padina vickersiae	x			
Order Chordariales				
Cladosiphon occidentalis	x			
Order Dictyosiphonales				
Stictyosiphon subsimplex	x			
**Myriotrichia subcorymbosa*	x			
Order Scytosiphonales				
Petalonia fascia	x		x	
Order Fucales				
Sargassum fluitans	x	x	x	x
S. natans	x	x	x	x
RHODOPHYTA				
Subclass Bangiophycidae				
Order Goniotrichales				
Asterocystis ramosa	x			
Goniotrichum alsidii	x	x	x	
Order Bangiales				
Erythrocladia subintegra	x	x	x	x
Erythrotrichia carnea	x	x	x	x
Bangia fuscopurpurea	x	x	x	x
Porphyra leucosticta	x			
Subclass Florideophycidae				
Order Nemaliales				
Acrochaetium spp.		?	x	x
A. flexuosum	x			
A. bisporum	x			
A. seriatum	x			
Order Gelidales				
Gelidium crinale	x	x	x	
Pterocladia bartlettii	x			
P. capillacea	x			
Order Cryptonemiales				
Heteroderma lejolisii	x			
Dermatolithon pustulatum	x			
Corallina cubensis	x			
***C. subulata*	x			
Jania capillacea	x			
Grateloupia filicina	x			

TABLE 3 (Continued)

	Port Aransas Edwards 1970	Freeport Keatts 1969	Galveston Lowe and Cox 1978	Louisiana Kapraum 1974
Order Gigartinales				
Solieria tenera	x			
Hypnea cornuta	x			
H. musciformis	x			
Neoagardhiella baileyi	x			
Gracilaria debilis	x			
G. foliifera	x	x	x	x
G. verrucosa	x			
Order Rhodymeniales				
Rhodymenia pseudopalmata	x			
Lomentaria baileyana	x			
Champia parvula	x			
Order Ceramiales				
Callithamnion byssoides	x			
Griffithsia tenuis	x			
Spermathamnion sp.	x			
Ceramium byssoideum	x			
C. fastigiatum	x			
C. strictum	x	x	x	
Centroceras clavulatum	x			
Spyridia aculeata	x			
S. filamentosa	x		x	
Polysiphonia boldii	x			
P. denudata	x	x	x	
P. echinata	x			
P. gorgoniae	x		x	
P. havanensis	x			x
P. subtilissima	x		x	x
P. tepida	x		x	
Bryocladia cuspidata	x	x	x	
B. thyrsigera	x			
Digenia simplex	x			
Bostrychia sp.				x
Chondria dasyphylla	x			
C. polyrhiza	x			
C. cnicophylla	x			
C. littoralis	x			
Laurencia poitei	x			

Key to Notation System X—Present ?—Probably present

*—*Corallina subulata* removed to *Haliptylon subulata* (Ellis et Soland) Johansen (Johansen, 1970).

**—*Myriotrichia* and *Stictyosiphon* have been indicated to be alternate forms in the life histories of other brown algae, i.e., *Hummia anusta* (Fiore, 1975); however, *Hummia* has not been found by the authors.

***—Using cultural studies, Yarish (1976) was able to identify several other epiphytic Chaetophoralean algae from Port Aransas. These include: *Ectochaete ramulosa, E. vagans, Pseudulvella prostrata, P. heterotricha, Entocladia testarum, Bulboceleon piliferum.* No valid comparisons can be made with other Texas or Louisiana sites until similar studies are made.

collections along the Louisiana coast. As with the Galveston studies, some species were collected infrequently or in very small numbers. Both areas have low species diversity. Tropical rhodophytes are further reduced on the Louisiana coast. Kapraun reported 9 species in 8 genera, compared with 14 species in 11 genera from Galveston. The coastal rhodophyte flora is of different composition in Louisiana than in Galveston. *Ceramium*, *Bryocladia*, and *Gelidium*, three of the most abundant rhodophytes of the Galveston area, were not encountered in Kapraun's investigation. *Polysiphonia subtilissima* and *Bangia fuscopurpurea* appear to be components of both costal communities.

Table 3 provides comparative species distribution information from studies of benthic marine algae in Texas and Louisiana. This table illustrates the reduction of species of benthic marine algae from Port Aransas, Texas to Galveston, Texas and to the Louisiana coast by comparing the data of Edwards (1970) at Port Aransas, Keats (1969) at Freeport, Lowe and Cox (1978) at Galveston, and Kapraun (1974) in Louisiana.

LITERATURE CITED

CONOVER, J. T. 1958. Seasonal growth of benthic marine plants as related to environmental factors in an estuary. *Publs Inst. mar. Sci. Univ. Tex.* **5**:97–147.

————. 1964. The ecology, seasonal periodicity and distribution of benthic plants in some Texas lagoons. *Bot. Mar.* **7**:4–41.

DAWES, C. J. 1974. *Marine Algae of the West Coast of Florida*. University of Miami Press, pp. 1–201.

DAWES, C. J. and J. F. van BREEDVELD. 1969. Benthic marine algae. In *Memoirs of the Hourglass Cruises*, Vol. 1, pt. 2, Florida Dept. Nat. Resources, St. Petersburg. 47 pp.

EDWARDS, P. 1969. Field and cultural studies on the seasonal periodicity of growth and reproduction of selected Texas benthic marine algae. *Contr. mar. Sci.* **14**:59–114.

————. 1970. Illustrated guide to the seaweeds and sea grasses in the vicinity of Port Aransas, Texas. *Contr. mar. sci.* Suppl. to Vol. **15**: (Reprinted 1976, 128 pp + addenda).

EDWARDS, P. and D. F. KAPRAUN. 1973. Benthic marine algal ecology in the Port Aransas, Texas area. *Contr. mar. Sci.* **17**:15–52.

EARLE, S. A. 1969. Phaeophyta of the eastern Gulf of Mexico. *Phycologia.* **7**(2):71–264.

————. 1972. Benthic algae and seagrasses—chemistry, primary productivity, and benthic algae of the Gulf of Mexico. **Folio 22** Serial Atlas of the Marine Environment. American Geographical Society.

FIORE, J. 1975. A new generic name for *Farlowiella musta* (Phaeophyta). *Taxon.* **24**: 497–498.

HUMM, H. J. 1956. Sea grasses of the northern Gulf coast. *Bull. mar. Sci. Gulf Caribb.* **4**: 305–308.

————. 1963. Some new records and range extensions of Florida Marine algae. *Bull. mar. Sci. Gulf Caribb.* **3**(4):516–526.

HUMM, J. H. and R. L. CAYLOR. 1957. The summer flora of the Mississippi sound. *Publs Inst. mar. Sci., Univ. Texas.* **4**:228–264.

HUMM, H. J. and R. M. DARNELL. 1959. A collection of marine algae from the Chandeleur Islands. *Pubs Inst. mar. Sci., Univ. Texas.* **6**:265–276.

HUMM, H. J. and H. H. HILDENBRAND. 1962. Marine algae from the Gulf Coast of Texas and Mexico. *Publs Inst. mar Sci., Univ. Texas.* **8**:227–268.

HUMM, H. J. and SYLVIA E. TAYLOR. 1961. Marine Chlorophyta of the upper west coast of Florida. *Bull. mar. Sci. Gulf Caribb.* **11**:321–380.

JOHANSEN, H. W. 1970. The diagnostic value of reproductive organs in some genera of articulated Coralline red algae. Br. Phycol. J. **5**(1):79–86.

KAPRAUN, D. F. 1970. Field and cultural studies of *Ulva* and *Enteromorpha* in the vicinity of Port Aransas, Texas. *Contr. mar. Sci.* **15**:205–285.

————. 1974. Seasonal periodicity and spatial distribution of benthic marine algae in Louisiana. *Contr. mar. Sci.* **18**:139–167.

KEATTS, H. 1969. Field observations from monthly collections of benthic algae at Freeport, Texas. Unpublished. Henry Keatts, Suffolk Co. Comm. College, Selden, L.I., N.Y.

SORENSEN, L.O. 1972. Preliminary check list of the sea grasses of Port Isabel, Texas. Unpublished. L. O. Sorensen, Pan Amer. Univ., Edinburg, Texas.

TAYLOR, W. R. 1954. Sketch of the character of the marine algal vegetation of the shores of the Gulf of Mexico. In P. S. Galstoff (ed.). Gulf of Mexico, its origin, waters and marine life. *U.S. Fish Bull.* **89**:177–192.

YARISH, C. 1976. Polymorphism of selected marine Chaetophoraceae (Chlorophyta). *Br. phycol. J.* **11**(1):29–38.

THE TOXIC EFFECTS OF THE WATER SOLUBLE FRACTIONS OF NO. 2 FUEL OIL AND OF THREE AROMATIC HYDROCARBONS ON THE BEHAVIOR AND SURVIVAL OF BARNACLE LARVAE[1]

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The deleterious effects of the water soluble fractions (WSF) of No. 2 fuel oil and of three aromatic hydrocarbons, namely naphthalene, benzene and toluene, on barnacle larvae were investigated. Freshly released nauplii of *Balanus eburneus* were used; the fuel oil was Exxon (Baytown). Dilutions of WSF of the oil and of saturated solutions of the aromatic hydrocarbons were made as required.

Nauplii were added to opaque black tubes containing test solutions in sea water; the tubes were illuminated from above. After 1 hr those larvae actively swimming were separated from those resting on the bottom; all larvae were counted. In other experiments mortalities were determined by vital staining with neutral red. All substances were most harmful when used immediately after preparation; their deleterious effects were less after storing them in a refrigerator. Furthermore, the fuel oil was much less harmful after it had been exposed to air for 3 days. In 1-hr experiments, half the larvae continued swimming at dilutions of stock solutions (WSF or saturated solutions) as follows: No. 2 fuel oil 12.5%; naphthalene 15%; toluene 12.5%; benzene 11%. The results were indicative of interference with swimming and phototactic behavior. Mortalities in 1-hr experiments did not exceed 13%.

From the results it is concluded that volatile aromatics, including naphthalene, toluene and benzene, are responsible for much of the deleterious effects on activity and survival of barnacle larvae. Comparisons are made with similar studies on other marine organisms.

INTRODUCTION

Pollutants affect animals in many ways, depending on the chemical species, concentration, etc. Behavior is altered, and the changes induced provide a useful indicator of the toxicity of the pollutant on the organism. It is well known that the meroplanktonic larvae of many marine invertebrates are attracted to light. Using barnacle larvae, I have studied changed phototactic responses in acute

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experiments to determine the toxicities of a petroleum oil and several light aromatic hydrocarbons. Mortalities of the larvae were also measured.

MATERIALS AND METHODS

Barnacles *Balanus eburneus* were collected from the stone jetties at Port Aransas. The animals were placed in large culture dishes containing offshore sea water 30‰ and the dishes were illuminated unilaterally by a 15 W fluorescent lamp (cold white light). Larvae aggregating on the illuminated side of the container were transferred through four changes of sea water; in the final solution there were 3 to 5 larvae per μl. The larvae were tested for a phototactic response over 72 hr and continued to show positive phototactic responses as shown in Fig. 1.

In order to study the effects of the pollutants, an apparatus was devised as follows. Eleven similar tubes of opaque black plastic were selected (140 mm long, internal diameter 3.5 mm). One end of the tube was fused to the terminal tapering portion of a Pasteur pipette with silicone adhesive (Fig. 2). The tubes were coated internally with a thin layer of silicone adhesive. A short piece of Tygon tubing was placed over the tip of the pipette, and the bottom was closed by a stopper. The tubes were placed in a rack, they were illuminated from above, and the lower portions were kept dark. Each tube contained 1.55 ml fluid to which was added 0.17 ml of fluid containing barnacle larvae.

Offshore filtered (Millipore 0.45 μm) sea water (30‰) was used for all experiments both for controls and for making up stock and test solutions. The petroleum oil tested was No. 2 fuel oil (Exxon Baytown). A stock solution was prepared by adding 1 part of fuel oil to 8 parts sea water (v/v) in a sealed vessel. It was slowly stirred by a magnetic stirrer for 24 hours, and the aqueous layer containing the water soluble fraction (WSF) was withdrawn and used as stock solution (Pulich *et al.* 1974). This solution was either used immediately or was stored in a refrigerator in a sealed container (maximum time 3 days). Containers were opened at the top

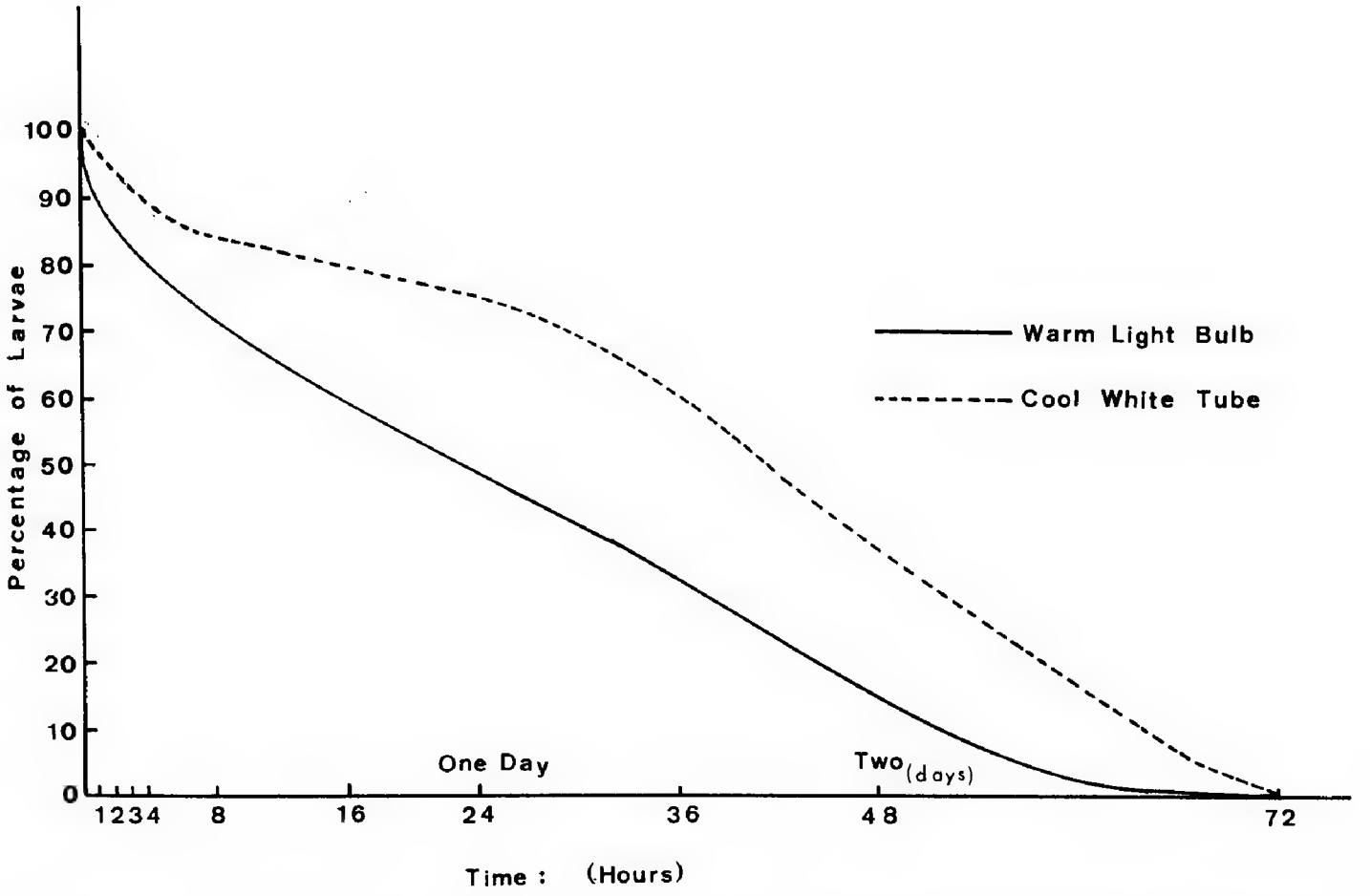

FIG. 1. Phototactic behavior of barnacle nauplii in culture dishes illuminated unilaterally by two kinds of lamps. The cool white fluorescent lamp gave higher survival of the larvae.

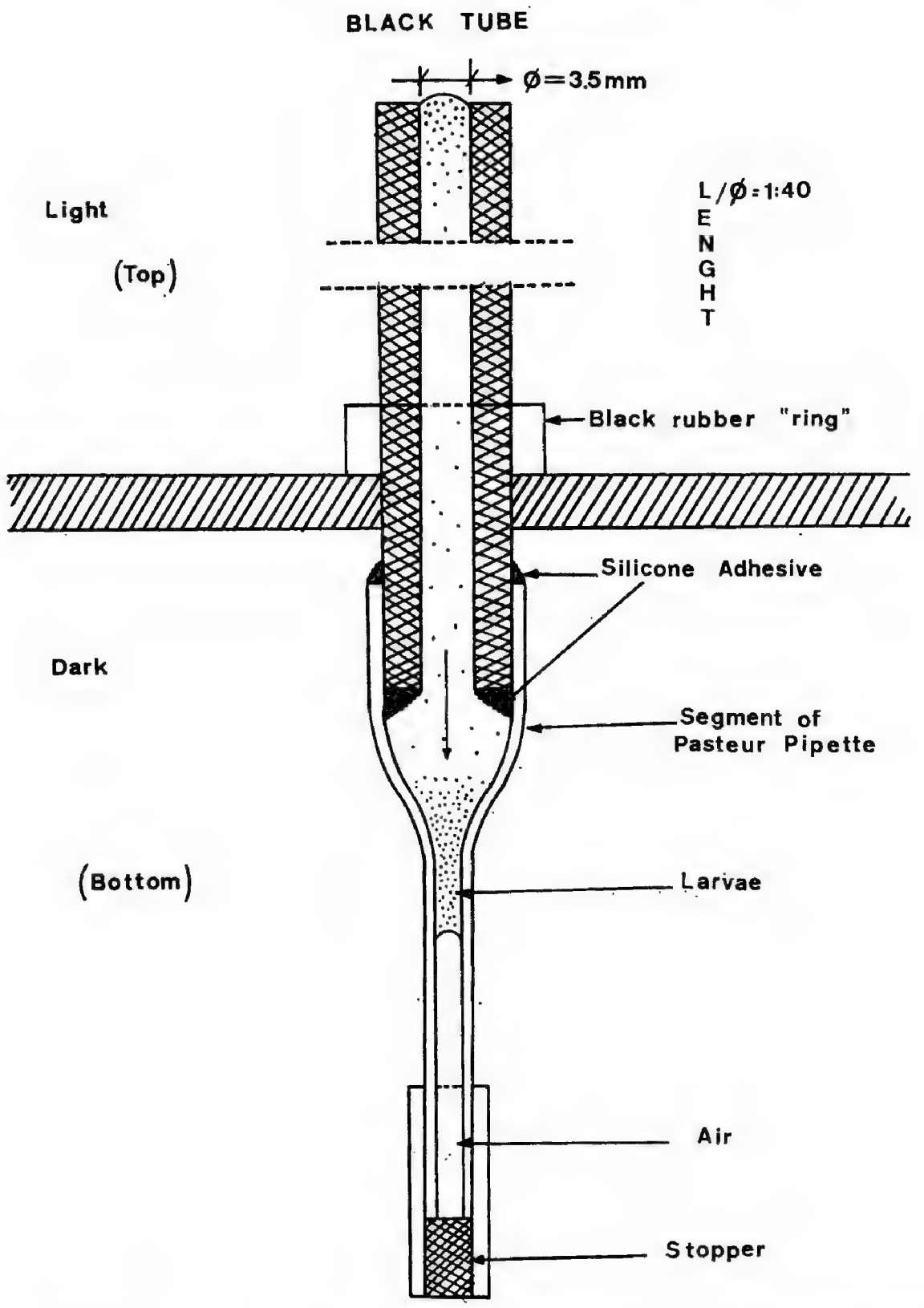

FIG. 2. Diagram of tubes used to test the influence of aqueous extracts of fuel oil and aromatic hydrocarbons on barnacle nauplii.

when fluid was withdrawn. The concentrations of total benzene extractable organics in the sea water soluble fraction of this fuel oil was 21 mg 1^{-1}; analyses of the chemical composition have been reported by Winters et al. (1976).

In later sections of this paper this value (of 21 mg 1^{-1}) is used for the concentration of extractable organics in the stock solution, and concentrations of those organics in diluted media are estimated from percentage dilutions on that basis.

Three aromatic hydrocarbons—benzene, toluene and naphthalene—were tested. They were added to sea water, about 20 ml 100 ml^{-1} of toluene and benzene (v/v), and 2.2 mg 100 ml^{-1} of naphthalene (w/v). The mixtures were shaken vigorously (260 rpm) for 1 hr on an "Eberbach" shaker, left standing for at least 30 min, and the fluid was withdrawn and filtered (What-

man No. 2). If not used immediately the solutions were stored in a refrigerator (maximum time 3 days). Stock solutions of fuel oil and aromatics were diluted with sea water (30‰) as required.

For the experiments two tubes (containing sea water) were used as controls, and nine (containing WSF—Water Soluble Fraction—or aromatics) were used for the experiment. The latter contained 10, 20, 30, 40, 50, 60, 70, 80 and 90% stock solution. Six drops containing approximately 100 larvae were added to each tube. The tubes (upper region) were exposed to light for 1 hr. When filling the tubes the meniscus of the fluid was raised above the top of the tube; it became level with the surface in 1 hr owing to exaporation. The lamp (15 W fluorescent cold white light) was positioned 33 cm from the tubes and on a level with their tops (Fig. 3). This position (0°, normal to the vertical) was important because the number of larvae attracted upwards changed as the position of the lamp was altered (Table 1). Replicates (2 to 5) were made of all experiments. Results with standard deviations are shown in the graphs (in Figs. 4 to 7). Experiments were carried out at 22°C in a dark room.

Figs 4 to 7. Results of experiments testing effects of aqueous extracts of fuel oil and aromatic hydrocarbons on barnacle nauplii in stock tubes. Concentrations of WSF at which one-third of the larvae were affected were 7.5%, 40.1% and 55%, in fresh, refrigerated and aerated media, respectively. Concentrations at which one-half the larvae were affected were

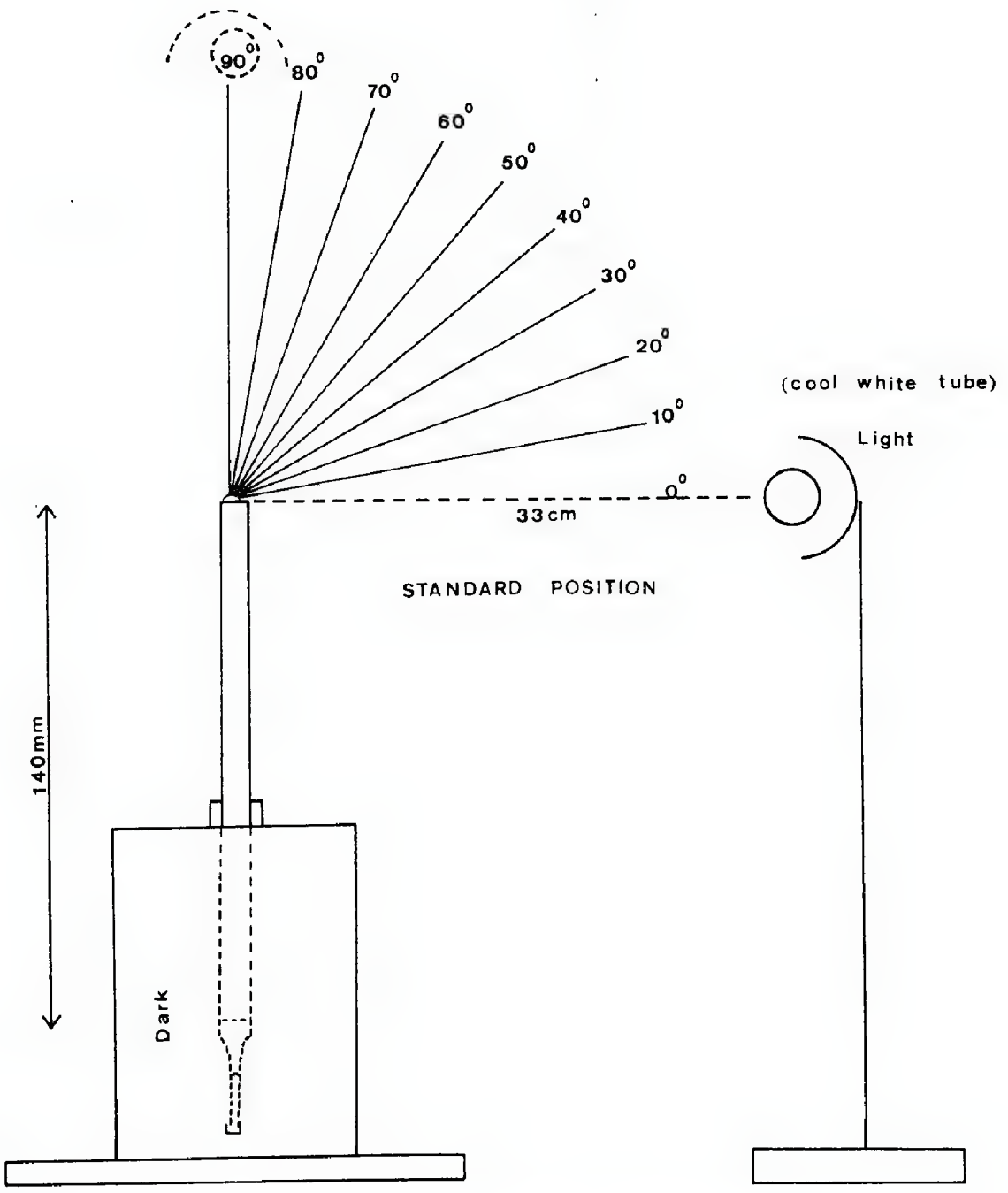

Fig. 3. Positioning of lamp relative to stock tubes used in the experiments.

TABLE 1

Effect of varying the height of the lamp on the proportion of larvae in the top fraction of the tubes.

Angle of lamp[1]	Proportion in top fraction		
Degree	Percentage larvae swimming on the top	Δ	Proportion in bottom fraction
0°	90.1/83.7[2]	6.4	13.1%
10°	86.5/81.5	5.0	16.0%
20°	83.8/79.3	4.5	18.45%
30°	81.1/77.6	3.5	20.65%
40°	79.8/77.7	2.1	21.25%
50°	76.4/74.2	2.2	24.7%
60°	74.2/72.1	2.1	26.85%
70°	74.5/71.9	2.6	26.8%
80°	72.6/70.3	2.3	28.55%
90°	70.3/67.0	3.3	31.3%

[1] 0° lamp normal to the vertical; 90° lamp vertically over the tubes.
[2] maximum/minimum.
Δ from maximum and minimum on the top.

12.5 and 47.5% in the first two media, respectively. Lines drawn visually. Vertical lines are standard deviation and numbers in parentheses denote numbers of observations.

At the end of each experiment the larvae lying at the bottom of the pipettes were separated from those actively swimming in the water column by discharging two drops of fluid from each pipette into a vial (bottom fraction). The larvae in the column (top fraction) were collected separately and formalin added to make a concentration of 10%. All larvae (top and bottom fractions) were counted in a Ward Zooplankton counting wheel No. 1810 (WILDCO Instruments—Aquatic Supply, Saginaw, Michigan).

To determine mortality in the bottom fraction the larvae were stained with neutral red, which colors only live larvae (Crippen and Perrier 1974). Two ml of sea water were added to the vial and 0.02 ml of a saturated solution of neutral red. The vial was slowly shaken and exposed to a fluorescent lamp for 6 hours, then 0.2 ml of formalin was added. After 5 min. all larvae were collected on a sieve, washed with water and placed in a small beaker. The water level was made up to 10 ml, and 0.5 ml of a saturated solution of acetic acid, sodium acetate and 1 ml of formalin were then added. The nauplii were placed in a refrigerator for several hours, or overnight, before counting. Live and dead larvae could be distinguished since the live larvae appeared more or less red, while the dead animals were white.

In another experiment the degree of evaporation of the volatile toxic substances in the WSF

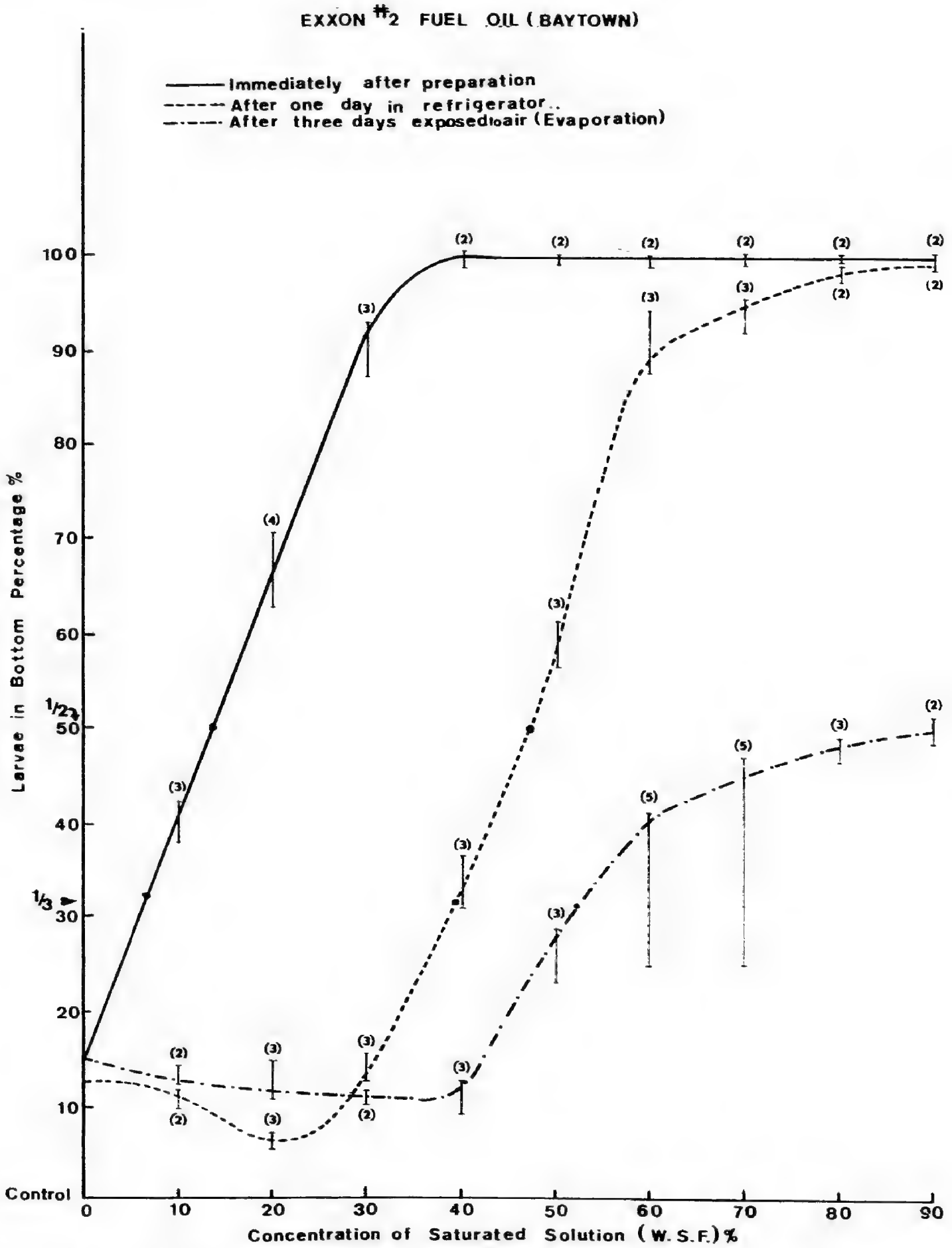

FIG. 4. No. 2 fuel oil: ——— used immediately after preparation; ..... used after storing in a refrigerator for 1 day; ——.——. used after exposure to air for 3 days.

FIG. 5

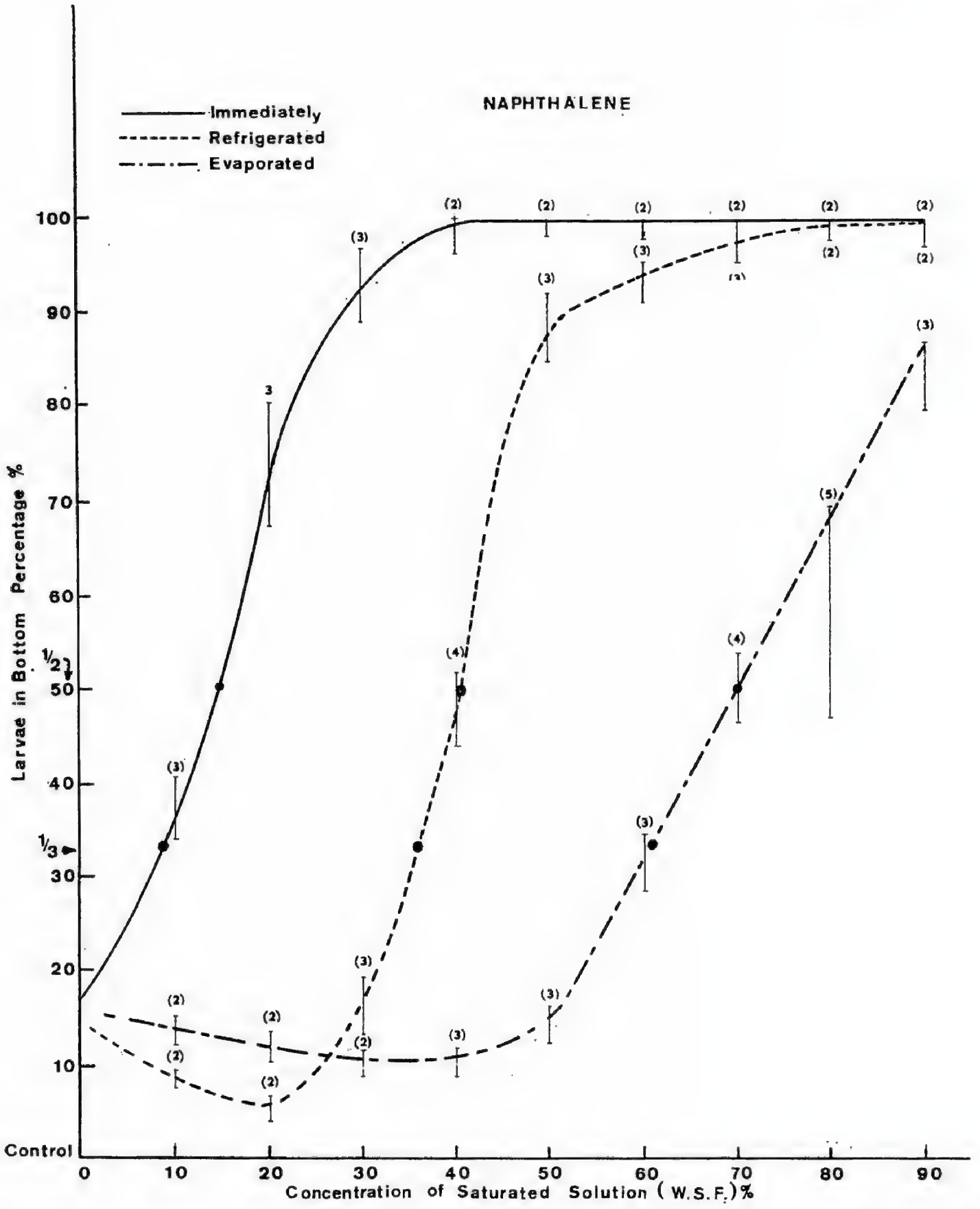

FIG. 5. Naphthalene: ——— used immediately after preparation; ..... used after storing in a refrigerator for 1 day; ——.——. used after exposure to air for 3 days.

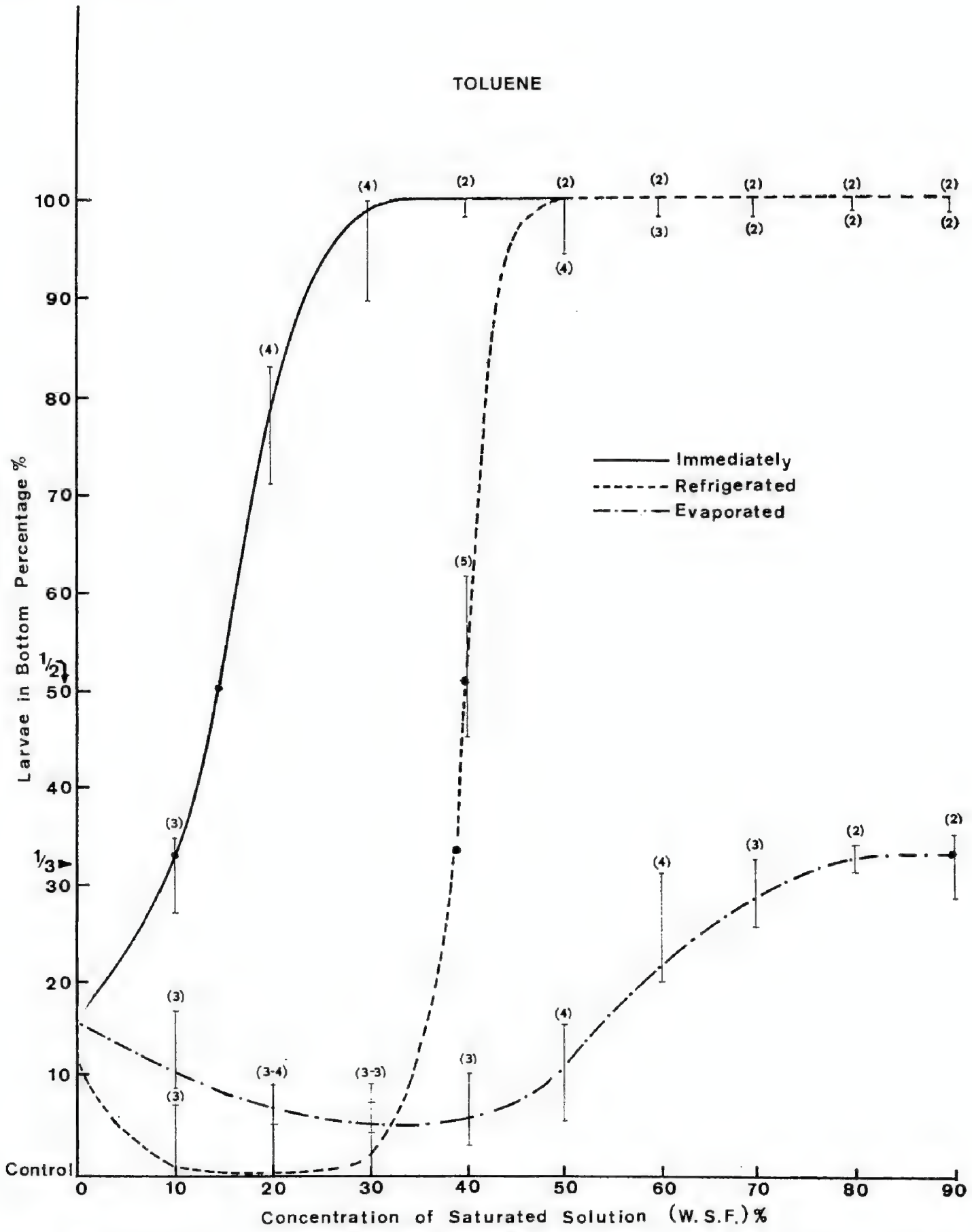

FIG. 6. Toluene: ——— used immediately after preparation; ..... used after storing in a refrigerator for 1 day; ———.———. used after exposure to air for 3 days.

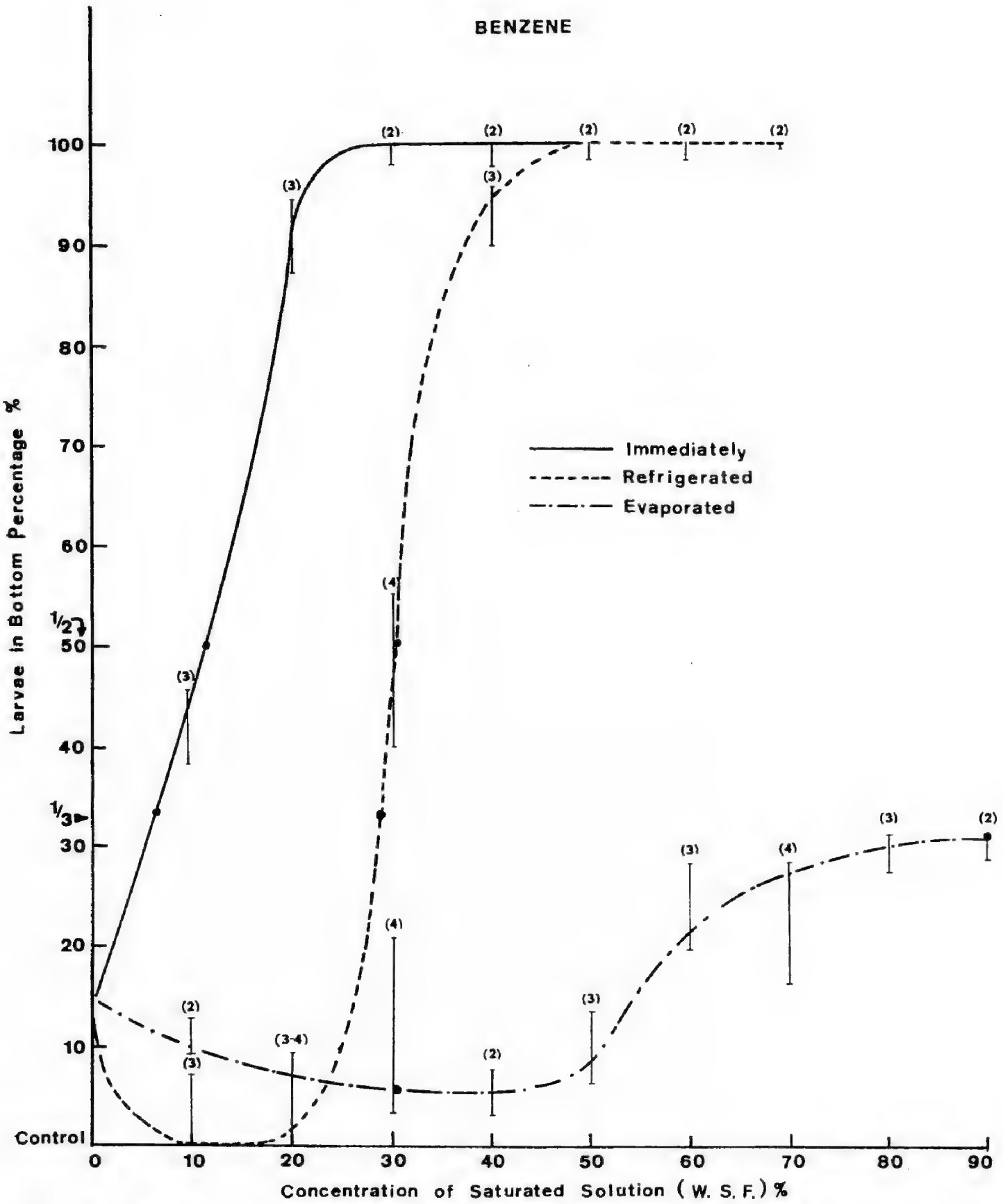

FIG. 7. Benzene: ——— used immediately after preparation; ..... used after storing in a refrigerator for 1 day; ———.———. used after exposure to air for 3 days.

was investigated by aerating a stock solution with an air-stone for 2, 6, and 24 hours. The deleterious effect of the solution aerated for 6 hours was equivalent to one exposed to air for 3 days.

OBSERVATIONS AND RESULTS

The results for behavioral responses are presented graphically in the curves of Figs. 4 to 7. All four substances affected phototactic and swimming activity to

a degree, depending upon the chemical species and the concentration. A peculiar effect in several cases at low concentrations was that more larvae occurred in the upper (swimming) fraction than in the controls, regardless of the chemical. The number of larvae lying on the bottom increased with higher concentrations of pollutants. For fuel oil the deleterious effects of solutions were in order: fresh solution > solution 1 day in refrigerator > solution exposed to air for 3 days. For aromatics the effects were in order: fresh solution > solution refrigerated 1 day > solution refrigerated 3 days. Concentrations at which half the larvae were affected are shown on the curves.

The same results were obtained from a stock solution aerated 6 hours with an air-stone, and the effects were greater after 2 hr aeration, and less after 24 hr.

Mortalities in the bottom fraction (Fig. 8) were low after 1 hr exposure, the mortality curves for all four substances were much the same. Even at the highest concentration used (90% of the stock solution) they did not exceed 13%.

For comparison, an experiment of survival is diluted sea water was carried out. Distilled water was used in lieu of stock solutions. Salinities were 3.3‰. Average mortality was 2.6%; median mortality was 6.9%.

DISCUSSION

The phototactic behavior and swimming activity of the nauplii were adversely affected by the water soluble extracts of No. 2 fuel oil and the three aromatic

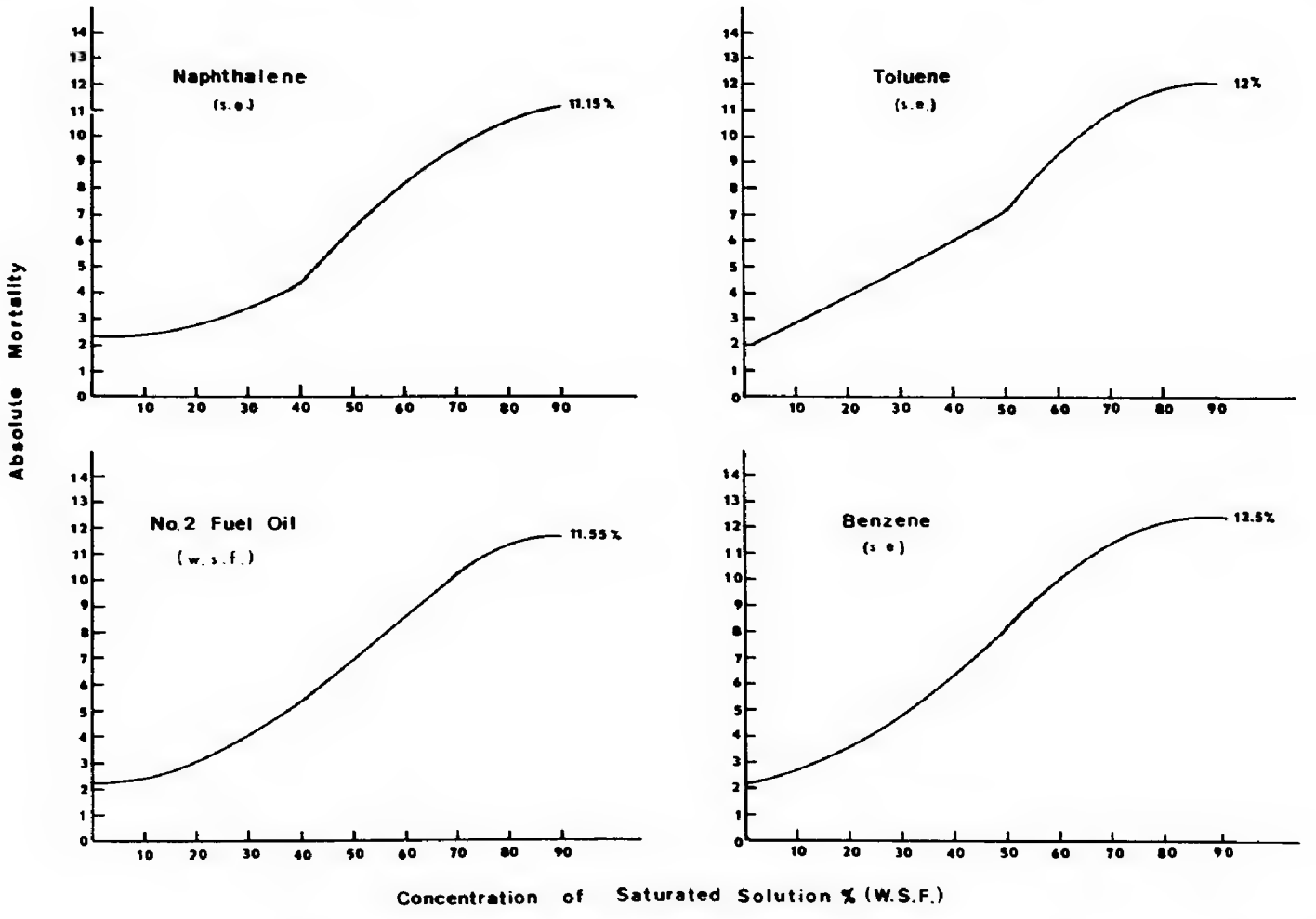

FIG. 8. Mortalities among larvae in the bottom fractions from the tubes used in the behavior experiments. Larvae were removed after 1 hour and stained for 6 hours. Mortality among the controls was 2%. Fresh solutions of the substances shown in the figure were used.

hydrocarbons (Fig. 9). Deleterious effects of No. 2 fuel oil on barnacle larvae were evident at the greatest dilution tested, viz. 10%, of a freshly prepared solution. Reduced activity also appeared at a level of about 40% WSF in the refrigerated sample and at about 50% WSF after exposure to air for three days.

In a study of the effects of petroleum oils on echinoid eggs, Allen (1971) tested a series of sixteen crude and refined oils using aqueous extracts prepared from 5% oil in sea-water. Most of the oils had little or no deleterious effects on these organisms; eleven, including some crudes and No. 2 fuel oil, began to show

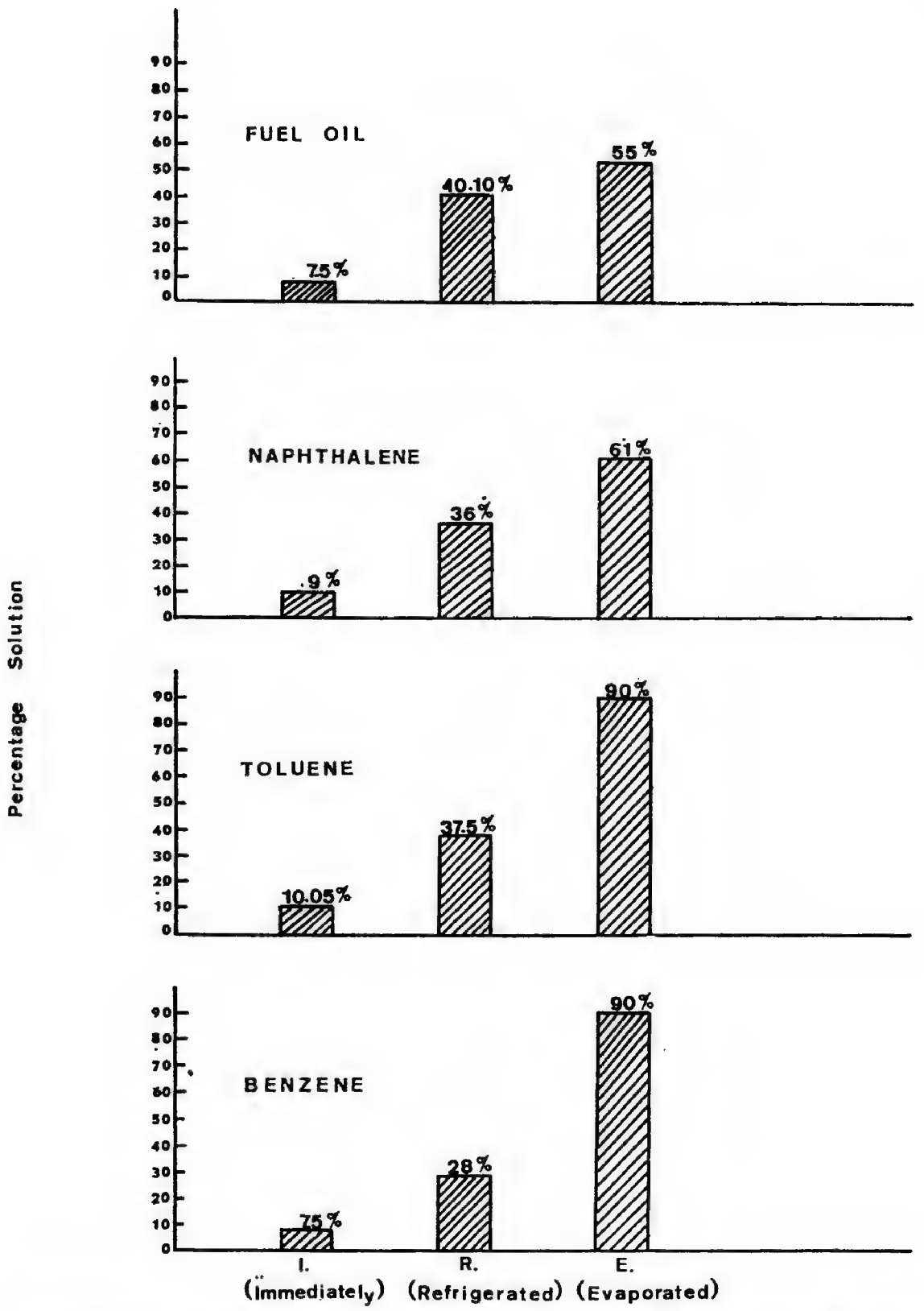

FIG. 9. Histogram showing the results of experiments using the tubes. The heights of the bars are the percentages of aqueous extracts or saturated solutions at which one-third the larvae were found in the bottom fractions. Substances are named in the figures.

adverse effects at concentrations of 5.9% of oil stock sea-water. On the assumptions that the concentration of measured hydrocarbons in the WSF of fresh fuel oil is 21 ppm in this study, an adverse effect on barnacle nauplii appears at about 2 ppm (10% WSF) and half the larvae are affected at 2.6 ppm (12.5%). Much higher concentrations of refrigerated and aerated samples are required to produce comparable effects (see Fig. 4). Analyses are not available for hydrocarbon content of the refrigerated and aerated media. Anderson *et al.* (1974), who tested a range of other marine invertebrates and some vertebrates in No. 2 fuel oil, obtained median toxic levels of 1.6 to 9 ppm.

Components of oils having immediate toxicity (acute effects) are low boiling saturated paraffins and aromatic hydrocarbons, both of which are partially water soluble (Nelson-Smith 1967; Blumer 1969, 1970). Analysis of Baytown No. 2 fuel indicate an aromatic content of 38% (Winters *et al.* 1976). Anderson *et al.* (1974) found that the aromatics were 13 times greater in the WSF than in the whole No. 2 fuel oil. Although some of the aromatics and their concentrations in the water soluble fractions are known, little evidence is as yet available as to their toxicities to marine animals.

These results show that the deleterious effects of No. 2 fuel oil are reduced after refrigeration and after exposure to air (Fig. 4). The changes very likely are due to evaporation or loss otherwise of the more volatile aromatic compounds. The light aromatic hydocarbons are believed to be the most toxic components of petroleum oils (Figs. 5 to 7).

The numbers of larvae in the bottom fraction were reduced in low concentrations of fuel oil exposed to air and in some of the aromatics (Figs. 4 to 7). No obvious explanation is available for this behavior although a stimulating effect on swimming at low concentrations is perhaps possible.

Concentrations at saturation of naphthalene, toluene and benzene is sea water 5 ‰, 5°C are 24.5, 22 and approximately 1550 ppm, respectively (Klevins 1950, Gordon and Thorne 1967, Polak and Lu 1973, Eganhose and Calder 1976, Sutton and Calder 1975). Using these values, estimated concentrations in ppm at which the behavior of half the larvae are affected are: fuel oil, 2.6;naphthalene, 3.6; toulene, 31.2; benzene, 17°. Ratios of concentrations at which half the larvae are affected relative to the amount of hydrocarbons present in a saturated solution are fuel oil, 0.13; napththalene, 0.15; toluene, 0.10; and benzene, 0.11.

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LITERATURE CITED

ALLEN, H. 1971. Effects of petroleum fractions on the early development of a sea urchin. *Mar. Pollut. Bull.* **2**:138–140.

ANDERSON, J. W., J. M. NEFF, B. A. COX, H. E. TATEM and G. M. HIGHTOWER. 1974. Characteristics of dispersions and water-soluble extracts of crude and refined oils and their toxicity to estuarine crustaceans and fish. *Mar. Biol.* **27**:75–88.

BLUMER, M. 1969. Oil pollution of the ocean. *Oceanus.* **15**(2):2–7.

————. 1970. Oil contamination and the living resources of the sea. *FAO Technical Conference on Marine Pollution and its Effects on Living Resources and Fishing.* Rome, Italy, 18–19 Dec. 1970. 11 pp.

CRIPPEN, R. W. and J. L. PERRIER. 1974. The use of neutral red and Evans blue for live-dead determination of marine plankton. *Stain Technology.* **49**(2):97–104.

EGANHOSE, R. P. and J. A. CALDER. 1976. The solubility of medium molecular weight aromatic hydrocarbons and the effects of hydrocarbon co-solutes and salinity. *Geochim. Cosmochim. Acta.* **41**:555–562.

GORDON, J. E. and R. L. THORNE. 1967. Salt effects on non-electrolyte activity coefficients in mixed aqueous electrolyte solutions. II. Artificial and natural sea water. *Geochim. Cosmochim. Acta* **31**:2433–2443.

KLEVINS, H. B. 1950. Solubilization of polycyclic hydrocarbons. *J. Phys. Chem.* **54**:283–298.

NELSON-SMITH, A. 1967. Oil, emulsifiers and marine life. *J. Devon Trust Nat. Conserv.* July (Suppl.):29–33.

POLAK, J. and LU, B.C.-Y. 1973. Mutual solubilities of hydrocarbon and water at 0 and 25°C. *Can. J. Chem.* **51**:4018–4023.

PULICH, W. M., JR., K. WINTERS and C. VAN BAALEN. 1974. The effects of a No. 2 fuel oil and two crude oils on the growth and photosynthesis of microalgae. *Mar. Biol.* **28**:87–94.

SUTTON, C. and J. A. CALDER. 1975. Solubility of alkyl benzenes in distilled water and sea water at 25°C. *J. Chem. Eng. Data.* **20**:320–322.

WINTERS, K., R. O'DONNELL, J. C. BATTERTON and C. VAN BAALEN. 1976. Water soluble components of four fuel oils: chemical characterization and effects on growth of microalgae. *Mar. Biol.* **36**:269–276.

A NEW SPECIES OF ASELLOTE MARINE ISOPOD, *MUNNA (UROMUNNA) HAYESI* (CRUSTACEA: ISOPODA) FROM TEXAS

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A new species of asellote isopod, *Munna (Uromunna) hayesi*, is described and illustrated. The species was found on algae-covered rocks on the south jetty at Port Aransas, Texas. It is the first of the genus *Munna* to be reported from the Gulf of Mexico, and the second species of the subgenus *Munna (Uromunna)* known from the western Atlantic.

INTRODUCTION

The genus *Munna* (sensu lato), Order Asellota, Family Munnidae, includes a large complex of more than 60 species of small marine and brackish water isopods. Attempts have been made to group the adequately described species into subgenera (Menzies 1962, Kussakin 1962, Frankenberg and Menzies 1966, Fresi and Mazzella 1974). The new species described herein is a member of the subgenus *Munna (Uromunna)* Menzies (1962). Only one species of this subgenus, *Munna (Uromunna) reynoldsi* Frankenberg and Menzies (1966), from salt marshes of Georgia, has previously been reported from the western Atlantic. The present species is the first record of the genus *Munna* (sensu lato) in the Gulf of Mexico.

Specimens were collected at the south jetty at Port Aransas, Texas during a field trip by a marine invertebrate zoology class from Lamar University. They were found in a sample obtained from the ship channel by several hauls of a small plankton net tossed out from the jetty. The isopods were probably dislodged as the net was pulled in over algae-covered rocks near the waterline.

The new species is named in honor of the late Dr. Edwin S. Hayes, former Head of the Biology Department and Dean of the College of Sciences at Lamar University.

MATERIAL EXAMINED

Port Aransas, Texas, channel side of south jetty; 5 Aug. 1975; in plankton sample taken from jetty rocks; 4 males, 2 females (one ovigerous), body length 0.95–1.05 mm.

Holotype: Male, length 1.05 mm, width 0.52 mm, deposited in the U. S. National Museum (Cat. No. USNM 1555297).

Allotype: Ovigerous female, length 1.0 mm, width 0.56 mm, deposited in the U.S. National Museum (Cat. No. USMM 155298).
Paratypes: One damaged male paratype and slides of dissected paratype material have been deposited in the U.S. National Museum (Cat. No. USNM 155299). The other partially dissected paratypes are deposited in the working collection, Department of Biology, Lamar University.

GENERIC CHARACTERIZATION

Genus **Munna** Krøyer, 1839

Diagnosis. Munnidae having coxal plates visible in dorsal view on pereonal somites two to seven inclusive. Body lacking spines. Eyes on a short immovable peduncle, preocular lobes generally present. Uropoda lacking peduncle. Antennae usually one-half or more the body length. (After Menzies, 1962).
Remarks. The present species differs from most of the other species of *Munna* in lacking distinct preocular lobes.

SUBGENERIC CHARACTERIZATION

Subgenus **Uromunna** Menzies, 1962

Diagnosis. *Munna* (sensu lato) with terminal joint of antennular flagellum never minute. Only one sensory filament on antennular flagellum. Mandibular palp comparatively short or absent. Exopod of pleopod 3 unjointed, narrower than the endopod. (After Fresi and Mazzella 1974).
Remarks. The subgeneric characters were recently reevaluated by Fresi and Mazzella (1974), who gave the revised diagnosis reproduced above. The present species agrees with their diagnosis, and resembles the only other western Atlantic species, *Munna* (*Uromunna*) *reynoldsi*, in lacking a mandibular palp. The present species has the apex of the first male pleopod more strongly expanded both laterally and distally than any of the other known species of *Munna* (*Uromunna*).

MUNNA (UROMUNNA) HAYESI N. SP.

Diagnosis

Munna (*Uromunna*) with front of cephalon straight and without distinct preocular lobes. First antenna with 6 segments, last article about 2/3 length of penultimate segment, and bearing one large sensory filament. Second antenna about 2/3 length of body, flagellum with 9–11 articles. First pereonite of male with elongated, rounded lateral margins. Pereonite 3 of female not markedly longer than adjacent segments. Mandibles lacking a palp. Ischium of pereopods with one prominent bifid seta on the superior margin. Pleotelson with continuous lateral margins lacking indentations for uropods, each ventrolateral border with about 11–14 ventrally directed, simple setae. Minute uropods inserted dorsally above and not projecting beyond lateral borders of pleotelson; exopod more or

less sub-cylindrical in cross-section, twice as long as broad, with 3–4 small setae near apex. Apex of first male pleopod expanded laterally as a short triangular process bearing 4 small setae; distal margin expanded posteriorly as a thin, leaf-like lobe devoid of setae. Endopod of second male pleopod an elongated cylindrical process tapering gradually to a narrow point.

Description

Cephalon. Front straight, without conspicuous setae. Eyes prominent on lateral protuberances; preocular lobes not evident.

Pereon. Pereonites 1–4 curved more or less anteriorly at the lateral margins, 5–7 curved posteriorly. A few short setae on lateral surfaces. Pereonite 1 of male (Fig. 1) with prominent elongated, rounded lateral margins. Pereonites 2–4 subequal in length. Female (Fig. 2) with pereonite 3 the broadest and somewhat the longest, but not markedly longer than adjacent segments.

Antenna 1 (Figs. 3, 4). Composed of 6 segments; terminal article about 2/3 length of penultimate segment, bearing one large sensory filament and 3 small setae at apex.

Antenna 2 (Fig. 5). Peduncle composed of 5 segments, last two subequal in length. No antennal scale is evident, although a seta is present where a scale has been detected in some other species. Flagellum consists of 9–11 articles.

Mandibles (Figs. 8–9). Left mandibular incisor with 3–4 teeth, lacinia with 4 teeth, setal row with 3 setae. Right mandibular incisor with 5 teeth, lacinia not present, setal row with 4 setae; neither mandible with palp.

Maxilla 1 (Fig. 10). Exopod with about 8–10 stout setae; endopod with 5 slender setae.

Maxilla 2 (Fig. 11). Trilobed; endopod with 2 longer and 1 shorter terminal setae, inner lobe of exopod with 3 terminal setae; outer lobe with 9–10 narrow setae along distal margin.

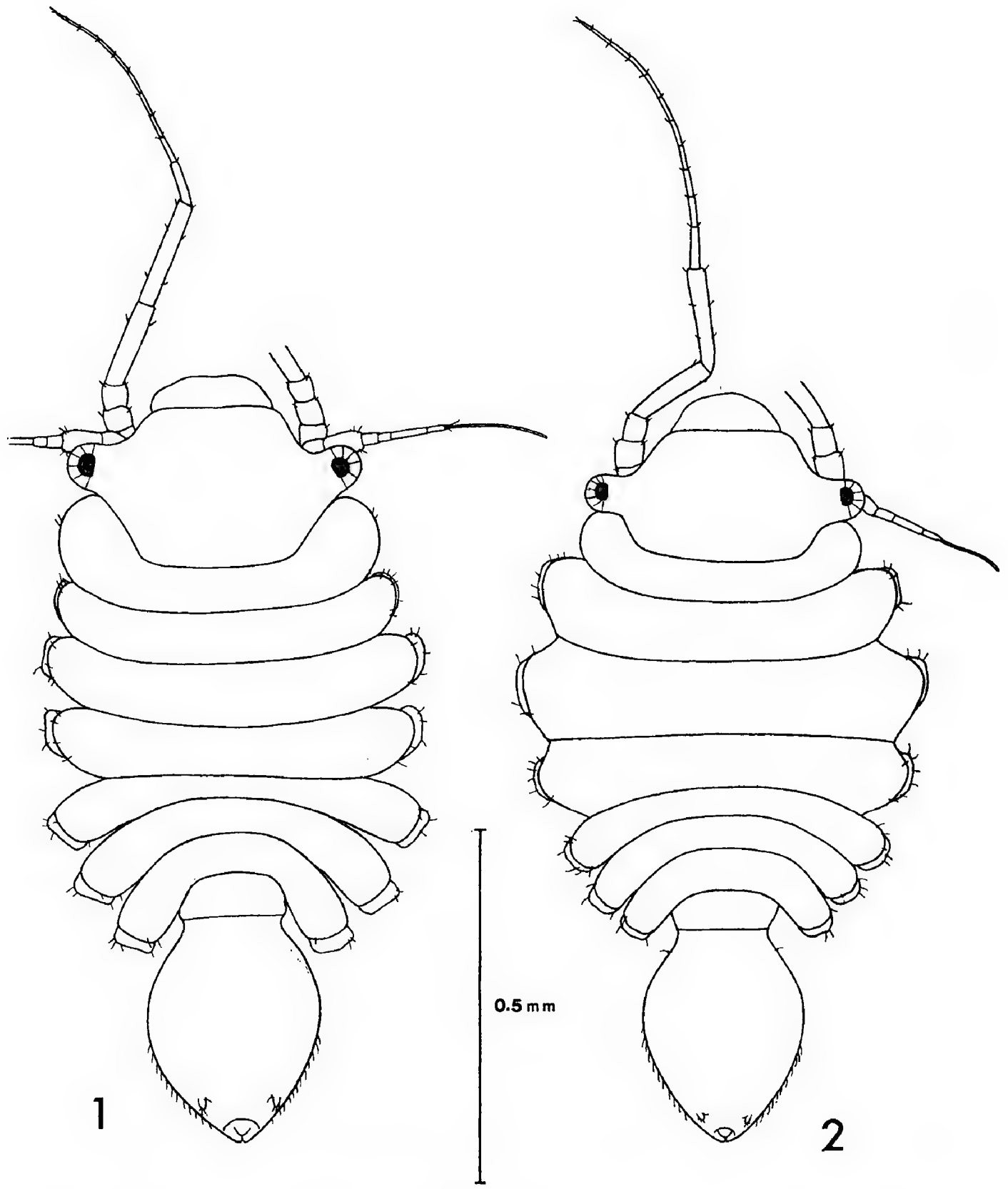
Maxilliped (Fig. 6). Palp with 5 articles, 2–3 expanded, each with 4 slender setae at inner distal corner; endognath with 3 coupling hooks.

Pereopod 1 (Fig. 12). More or less similar in male and female. Propodus broad, about as long as carpus and merus combined. Outer distal corner of merus with 3 stout bifid setae, inner distal corner with 1. Inner margin of carpus with 2 bifid setae, and 2 more at inner distal corner. Inner margin of propodus with about 3 bifid setae and a few simple setae.

Pereopod 7 of male (Fig. 7). Propodus about 1⅓ times as long as carpus. Propodus with about 7 stout bifid setae on inferior margin and about 8 mostly simple setae on superior margin. Merus about ½ as long as carpus, with 2 long bifid setae at superior distal corner and 1 bifid seta on inferior margin. Ischium with 1 prominent bifid seta on the superior margin at about the proximal third of its length, and a few small simple setae.

Other pereopods. The number of setae shows some variation.

Pleotelson (Figs. 18, 19). Vaulted, with continuous lateral margins lacking indentations for uropods; each ventrolateral margin bears about 11–14 ventrally

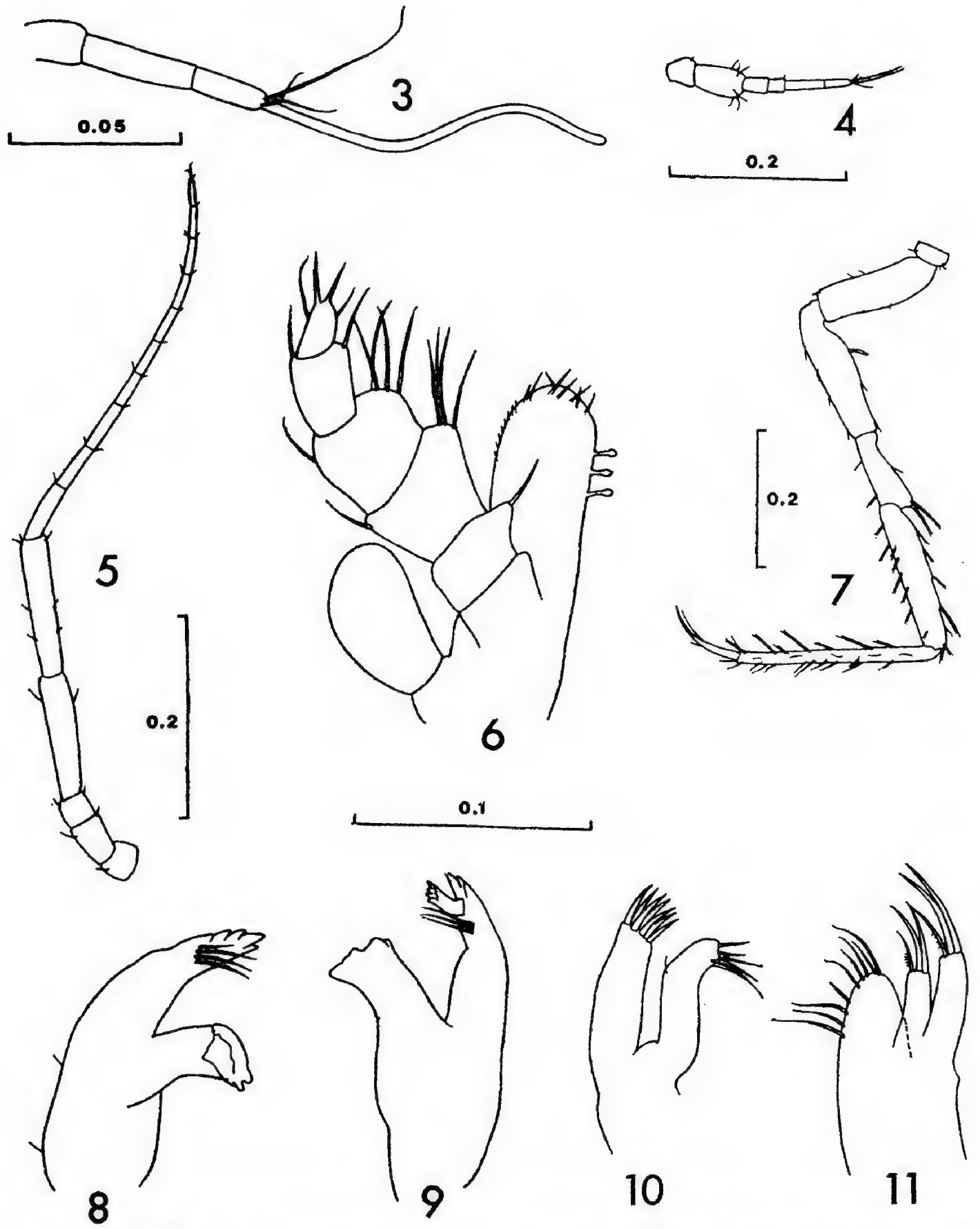


FIGS. 1–2. *Munna* (*Uromunna*) *hayesi* n. sp. 1, Male paratype, length 1.05 mm; 2, Female allotype, length 1.0 mm.

directed, simple setae. Apex with a small median projection dorsally; ventral apex shallowly cleft.

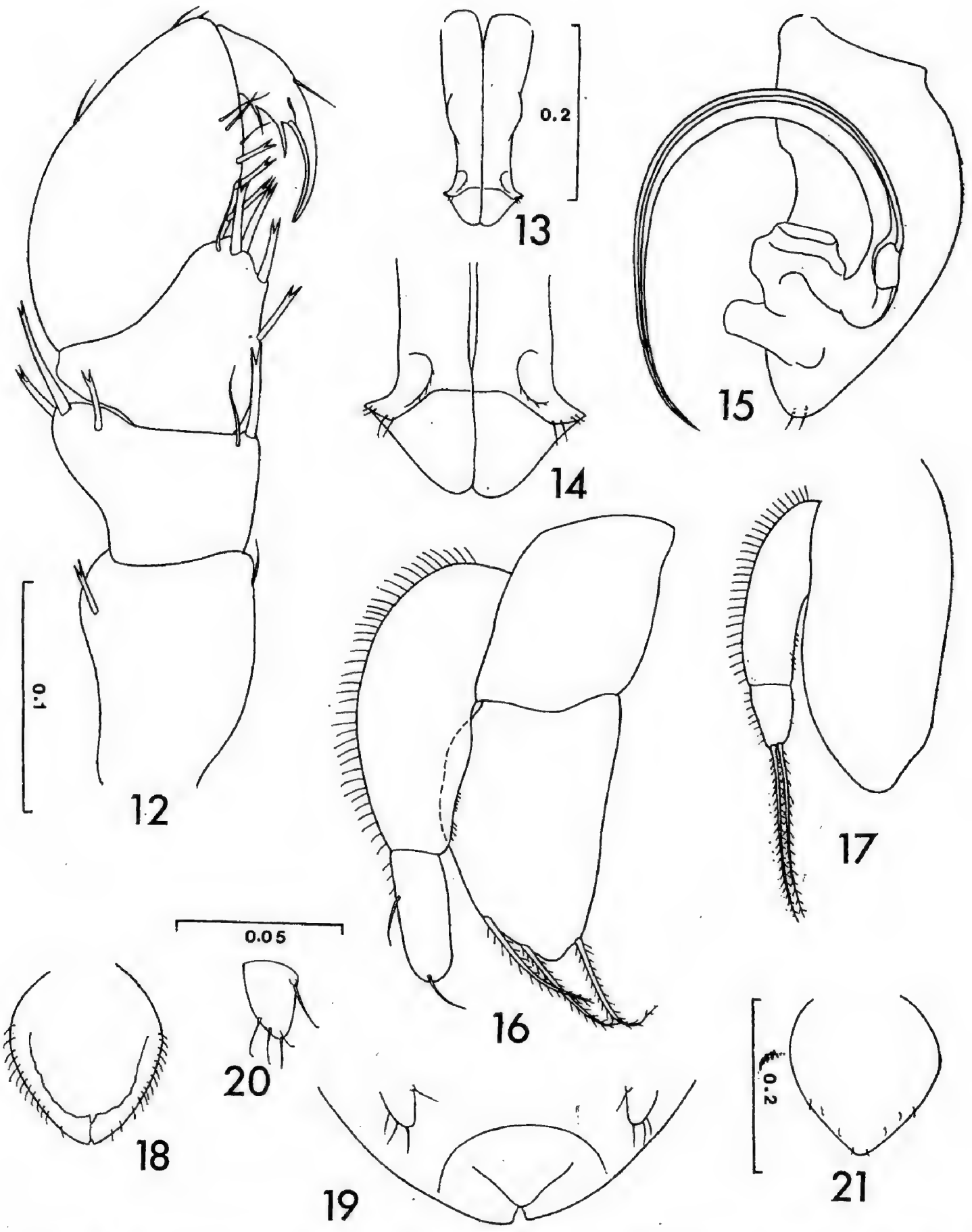
Uropods (Fig. 20). Very short, not projecting beyond lateral borders of pleotelson. Endopod minute, with a single apical seta. Exopod more or less subcylindrical, twice as long as broad, with 3–4 small setae near distal end.

Male pleopod 1 (Figs. 13, 14). Apex with the lateral corner flared outward as a



FIGS. 3–11. *Munna* (*Uromunna*) *haysei* n. sp. 3, Apex of first antenna, male paratype; 4, First antenna, male paratype; 5, Second antenna, female allotype; 6, maxilliped, male paratype; 7, Seventh pereopod, male paratype; 8, Right mandible, male paratype; 9, Left mandible, male paratype; 10, First maxilla, male paratype; 11. Second maxilla, female paratype. (Scales in mm; 8–11 same as 6; others as indicated.)

short triangular process bearing 4 small setae; distal end expanded posteriorly as a thin, leaflike lobe devoid of setae.



FIGS. 12–21. *Munna* (*Uromunna*) *hayesi* n. sp. 12, First pereopod, male paratype; 13, First pleopods, male paratype; 14, Same, detail of apex; 15, Second pleopod, male paratype; 16, Third pleopod, male paratype; 17, Fourth pleopod, male paratype; 18,Pleotelson, male paratype, ventral; 19, Pleotelson, male paratype, detail of apex, dorsal; 20, Uropod, male paratype; 21, Second pleopod, female paratype. (Scales in mm; 14–17 and 19 same as 12; 18 same as 21; 13 and 20 as indicated.)

Male pleopod 2 (Fig. 15). Exopod lacks plumose distal setae; endopod long, cylindrical, tapering to a narrow point.
Male pleopod 3 (Fig. 16). Endopod broader than exopod and bears 3 plumose setae at apex.
Male pleopod 4 (Fig. 17). Endopod broader than exopod and lacks distal setae; exopod bears 2 terminal plumose setae.
Female pleopod 2 (Fig. 21). About as long as wide, tapering to an obtuse apex, with about 4 minute setae near each lateral border.

AFFINITIES

The present species differs from all other known species referred to this subgenus in the degree of lateral and distal expansion of the first male pleopod. It seems closest to *Munna* (*Uromunna*) *reynoldsi* in having the frontal margin of cephalon straight, mandibles lacking a palp, uropodal exopod more or less subcylindrical, and lateral margins of pleotelson with several setae but without serrations. The two differ, however, in several readily observable features, as well as in certain details of the appendages. The following key allows easy separation of the two western Atlantic species of *Munna* (*Uromunna*) with a minimum of dissection.

KEY TO THE WESTERN ATLANTIC SPECIES OF MUNNA (UROMUNNA)

—Lateral borders of pleotelson with indentations for uropods, which project beyond margin of pleotelson; body length greater than twice the width; lateral margin of first pereonite of male not distinctly longer than those of other pereonites; third pereonite of female about twice the length of any other; apex of first male pleopod simple.

Munna (Uromunna) reynoldsi Frankenberg and Menzies, 1966.
Salt marshes along the coast of Georgia

—Lateral borders of pleotelson without indentations for uropods, which do not project beyond margin of pleotelson; body length not more than twice the width; lateral margin of first pereonite of male distincly longer than those of other pereonites; third pereonite of female not much longer than any other; apex of first male pleopod expanded.

Munna (Uromunna) hayesi n. sp. Algae-covered rocks
on jetty at Port Aransas, Texas

LITERATURE CITED

FRANKENBERG, D. and R. J. MENZIES. 1966. A new species of asellote marine isopod, *Munna* (*Uromunna*) *reynoldsi* (Crustacea: Isopoda). *Bull. mar. Sci.* **16**:200–208.

FRESI, E. and L. MAZZELLA. 1974. The genus *Munna* Krøyer (Isopoda: Asellota) in the Island of Ischia. *Pubbl. Staz. zool. Napoli.* **39**:44–63 (1971).

KUSSAKIN, O. G. 1962. On the fauna Munnidae (Isopoda, Asellota) from the far eastern seas of the U. S. S. R. *Trudy zool. Inst., Leningr.* **30**:17–65. (In Russian.)

MENZIES, R. J. 1962. The zoogeography, ecology and systematics of the Chilean marine isopods. *Repts. Lund Univ. Chile Exped. 1948–49.* **42**:1–162.

TWO NEW SPECIES OF HAUSTORIID AMPHIPODS (CRUSTACEA: AMPHIPODA) FROM THE NORTHWESTERN GULF OF MEXICO

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Two new species of sand-burrowing amphipods of the family Haustoriidae (Subfamily Haustoriinae) from the Texas coast are described and illustrated. *Protohaustorius bousfieldi* n. sp. occurs in clean to muddy sand of Gulf beaches from the lowest intertidal levels to offshore depths of at least seven meters. *P. bousfieldi* is distinguished by the broad posterior margin and spination of the merus of peraeopod 7, small number of plumes at posterior angle of coxae 1, 2, and 3, small number of mandibular palp comb spines, sparsely spinose posterior margin of uropod 1 peduncle, poorly developed inner plate of maxilla 1, and narrow, relatively deeply cleft telson. *Parahaustorius obliquus* n. sp. is found on wave-exposed sand beaches from the lower intertidal to subtidal depths. *P. obliquus* is closely related to *P. longimerus* Bousfield 1965, but is distinguished by the smaller adult size, shape and spination of the posterior margin of merus of peraeopod 7, greater medial width of head, and details of certain appendages.

INTRODUCTION

The family Haustoriidae is a morphologically primitive group of gammaridean Amphipoda adapted for burrowing. The subfamily Haustoriinae includes the more specialized members, many adapted for filter-feeding, which inhabit the harsh sandy-beach environment. The ecology of several Atlantic coast species has been studied in considerable detail by various workers (e.g., Croker 1967; Dexter 1967, 1971; Sameoto 1969; Bousfield 1970; Howard and Elders 1970; Ivester and Coull 1975; Holland and Polgar 1976).

Adaptive radiation in the subfamily Haustoriinae is proceeding most actively in the cool to warm-temperate regions of the North American Atlantic and Gulf coasts, where about 28 species in seven genera are known to occur. Six of these genera are represented both on the Atlantic coast and in the Gulf of Mexico, but the species show a highly endemic distribution. Apparently only one of about 16 Gulf species (all but one of which are undescribed) occurs on the Atlantic coast, and none of the other Atlantic species are found in the Gulf (Bousfield 1970, and personal communication).

During recent studies of the beach fauna of the Texas coast we collected several of the undescribed Gulf species of Haustoriinae, which we will describe in a series of papers. Our preliminary data indicate that haustoriid amphipods comprise a large fraction of the intertidal biomass on Texas beaches.

One new species each in the genera *Protohaustorius* and *Parahaustorius* are reported in the present paper. The new species of *Protohaustorius* was found inshore at Sea Rim State Park and Point Bolivar, and at one offshore station about 29 km south of Sabine Pass. The genus *Protohaustorius* is considered by Bousfield (1970) to be the most primitive, least specialized member of the Haustoriinae, and closest to the stock from which other North American genera have radiated. The new species of *Parahaustorius* was collected at several wave-exposed sandy beaches between Sea Rim State Park and north Padre Island. *Parahaustorius* is one of the less specialized genera of Haustoriinae, but shows a greater specialization of mouthparts than *Protohaustorius*.

We are most grateful to Dr. E. L. Bousfield for critically reviewing the manuscript, and for providing encouragement and much helpful information for the study.

GENERIC CHARACTERIZATION

Genus **Protohaustorius** Bousfield 1965

Body relatively narrow; head narrow, rostrum short. Pleosome not overhanging urosome. Antenna 1, penduncular segment 1 longest; accessory flagellum 2-segmented. Antenna 2, peduncle 4 shallow-lobate behind; flagellar segment 1 elongate.

Mandible, incisor bidentate. Maxilla 2, outer plate little expanded. Maxilliped, segment 3 clavate.

Gnathopod 2, segment 6 much shorter than 5. Peraeopods 3 and 4 similar; peraeopod 4 longer and stouter (esp. segment 4) than peraeopod 3.

Abdominal side plate 3 rounded behind. Urosome large; uropod 1, peduncle large, biramous; uropod 2 biramous, small; uropod 3 biramous, terminal segment of outer ramus relatively short. Telson entire, slightly cleft. (After Bousfield 1973).

Remarks: The new species conforms to the above diagnosis, except that the telson is cleft nearly halfway to the base.

PROTOHAUSTORIUS BOUSFIELDI NEW SPECIES

Material Examined

Southern tip of Bolivar Peninsula, 1–2 km north of jetty, fine-grained sandy beach grading to semi-protected flats of muddy sand, water depth a few cm to 1 meter, 17 Oct. 1975, PBR and CRS: 6 ♀ ♀ (5 ovig.), length 2.7–3.4 mm, 4 ♂ ♂, 2.6–2.8 mm; same approximate locality, muddy sand, slight wave exposure at seaward edge of intertidal flat, water depth 30–60 cm. 21 Aug. 1976, PBR, Tammy Hiertzler, Julie Rose: 1 ♀, 14 ♂ ♂, 2.2–2.8 mm, 22 imm.; Port Bolivar opposite dump road, clean sand in surf, water depth 0.6–1 m, 21 Aug. 1976, PBR, TH, JR: 2 ♀ ♀ (ovig.), 3.1, 3.4 mm, 3 ♂ ♂, 2.4–2.7 mm, 6 imm.; Sea Rim State Park, clean sand in surf, water depth 1.5 meters, 29 May 1976, PBR: 4 ♀ ♀ (3 ovig.), 2.5–2.9 mm, 6 ♂ ♂, 1.9–2.9 mm; same approximate locality, water depth 60 cm, 5 Sept. 1976, PBR: 10 ♀ ♀ (ovig.), 2.8–3.1 mm, 5

♂ ♂, 2.1–2.4 mm; same locality, water depth a few cm, 9 Oct. 1976, PBR: 5 ♀ ♀ (4 ovig.), 3.2–4.1 mm, 8 ♂ ♂, 2.5–3.0 mm, 1 imm.; Gulf of Mexico 29 km south of Sabine Pass, Texas, on Sabine Bank, clean sand, water depth 6–7 meters, 11 Aug. 1975, *Whooping Crain*[1]: 2 ♀ ♀, 3.2, 4.1 mm.

Holotype: Ovigerous female, 3.2 mm, deposited in the U. S. National Museum (USNM 170252).

Paratypes: Ovigerous female, 3.2 mm, male, 2.6 mm, and slides of dissected parts, deposited in the U. S. National Museum (USNM 170253); ovigerous female, 3.2 mm, male, 2.6 mm, and slides of dissected parts, deposited in the National Museum of Natural Sciences (Canada).

Type locality: Southern tip of Bolivar Peninsula, 1–2 km north of jetty at Bolivar Roads, Texas.

Ecology: Clean fine-grained sand in surf of open Gulf beaches to muddy sand of partially sheltered flats, from lowest intertidal to offshore depths.

The new species is named in honor of Dr. E. L. Bousfield, who has contributed greatly to knowledge of Haustoriidae and other Amphipoda.

Remarks: This species often co-occurred with undescribed species of *Acanthohaustorius*.

Diagnosis

Head slightly broader than long. Antenna 1 flagellum 4-segmented. Antenna 2, peduncle segment 4 posterior lobe long axis parallel to anterior margin; flagellum 1st article distinctly broader than following segments. Mandibular palp, segment 3 with 2–4 proximal marginal comb spines. Maxilla 1, inner plate weakly developed, with one seta. Coxa 1, 2, and 3, posterior angle with 1, 2, and 1 plumes, respectively. Peraeopod 4, coxal plate produced posteriorly, subacute, about 1.25 times broader than long. Peraeopod 5, segment 4 little broader than 5. Peraeopod 6, segment 5 subrectangular, distal margin with shallow U-shaped incision; segment 6 shorter than 5, posterior margin bare. Peraeopod 7, basis proximal posterior margin sharply incised; segment 4 posterior border at least as wide as anterior border, somewhat oblique, with 3 (sometimes 4) spines above lower angle. Pleosome side plate 3, anteroventral margin nearly straight. Pleopods, outer ramus 9–13 segmented, inner 6–9 segmented. Uropod 1, posterior margin of peduncle with 1 stout spine proximally, separated by gap from next 2 to 3 marginal spines before 3 large inter-ramal spines. Uropod 3, terminal segment of outer ramus distincly shorter than peduncle. Telson narrow, with narrow V-cleft extending nearly halfway to base; proximal margins subparallel; each lobe with 3 unequal apical spines.

Description

Male (1.9–3.0 mm) smaller but similar to female (2.7–4.1 mm). Head (Fig. 1, C). Broader than long, broadest posteriorly. Antennal sinus shallow, rostrum broad, obtuse. Eyes in life circular, prominent, but inconspicuous in preserved

[1] A shrimp trawler named after the owner, Mr. Donald Crain of Sabine Pass, Texas.

material. Antenna 1 (Fig. 1, A). Peduncular segment 1 with 5 lateral plumes; segment 2 slightly expanded distally, anterior border with 8 plumes, posterior border with 1 plume near margin proximal to distal group. Flagellum 4-segmented, 1st article about twice length of second; a few slender calceoli present.

Antenna 2 (Fig. 1, B). Peduncular segment 4, posterior margin with about 13 plumes, few setae on dorsal face; posterior lobe long axis parallel to anterior margin. Segment 5 relatively broad. Flagellum 4-segmented, 1st article much the broadest, twice the length of segment 2; calceoli lacking.

Upper lip (Fig. 1, D). Apex smooth, with one minute seta.

Lower lip (Fig. 1, E). Inner lobes relatively short, apically broad.

Mandible (Fig. 1, F). With 3 accessory blades; palp segment 3 with 2–4 short comb spines proximally and 8 apical spines; 2nd article with 1–2 simple setae.

Maxilla 1 (Fig. 1, G). Inner plate feebly developed as a small rounded lobe with 1 apical seta; accessory lobe vestigial.

Maxilla 2 (Fig. 1, H). Outer plate with about 10 pectinate and 2 plumose inner marginal setae.

Maxilliped (Fig. 1, I). Palp segment 3 short clavate, rounded distally.
Gnathopod 1 (Fig. 2, A). Posterior angle of coxa with 1 plume. Segment 2 posterior margin with 3 plumes, and 2 at distal angle. Segment 5 relatively short, broad, anterior border bare. Segment 6 short, broad; apical nail blunt conical.

Gnathopod 2 (Fig. 2, B). Posterior angle of coxa with 2 plumes. Segment 2 slightly sinuous, posterior border with 3–5 setae and group at distal end. Segment 5 relatively long, with 4 comb spines ventrodistally. Segment 6 stout, minutely subchelate. Female brood plate short, with about 7 marginal setae.

Peraeopod 3 (Fig. 2, C). Posterior angle of coxa with 1 long naked seta and 1 smaller plume. Segment 4 slender, anterior margin bare, posterior border with 3 to 4 groups of plumes. Segment 5 posterior lobe with 6 spines and 3 plumes. Segment 6 with 9 marginal spines. Female brood plate with about 15 marginal setae.

Peraeopod 4 (Fig. 2, D). Coxal plate produced posteriorly, subacute, about 1.25 times broader than long, lower margin convex. Segment 4 stout, anterior margin bare, posterior margin with 4 plumes, and 2 at distal angle. Segment 5 with 7 spines; segment 6 with 12–14 marginal spines. Female brood plate with about 14 marginal setae.

Peraeopod 5 (Fig. 2, E). Coxal lobes broad, produced anteriorly to obtuse apex. Segment 2 narrowing distally, posterior margin bare, anterior margin with 4 plumes. Segment 4 little broader than subquadrate segment 5. Segment 6 slender, slightly longer than 5, anterior border with 2 (occasionally 3) spine groups.

Peraeopod 6 (Fig. 2, F). Posterior coxal lobe large, produced posteriorly, 1 small seta on lower margin. Segment 2 anterior border with about 10 plumes. Segment 4 broadest distally, about 1.6 times length of segment 5, lateral face

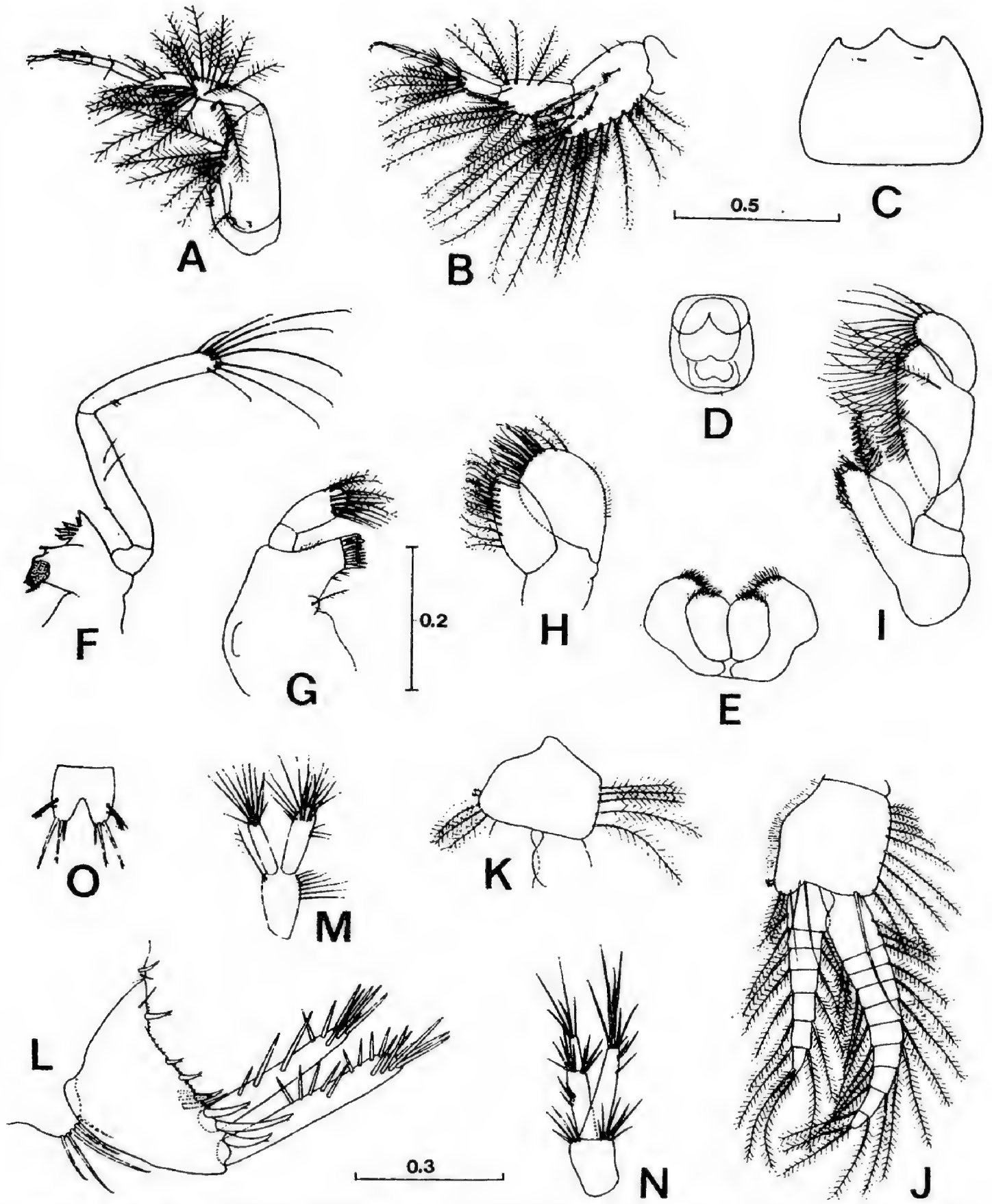

FIG. 1. *Protohaustorius bousfieldi* n. sp., all female paratype (ovigerous), except D, from male paratype. A, antenna 1; B, antenna 2; C, head; D. upper lip; E. lower lip; F, left mandible; G, maxilla 1; H, maxilla 2; I, maxilliped; J, pleopod 1; K, pleopod 3, peduncle; L, uropod 1; M, uropod 2; N, uropod 3; O, telson. Scale lines in mm; scales A-B same as C; D-F, J-O same as L; I same as G-H.

with one longitudinal row of spines anteriorly. Segment 5 subrectangular, distal margin with shallow U-shaped incision. Segment 6 slender, distinctly shorter than segment 5, both margins bare.

Peraeopod 7 (Fig. 2, G). Coxal plate shallow, narrowing to obtuse posterior apex, with 1 small seta. Basis proximal posterior margin with a sharp incision. Segment 4 posterior border at least as wide as anterior border, but oblique rather than truncate, with 3 to 4 stout spines above lower angle. Segment 6 relatively narrow, slightly shorter than segment 5; posterior margin with 5–6 spine groups, anterior border with 4–5.

Pleosome side plate 3 (Fig. 2, H). Anteroventral margin nearly straight, with a few plumes; lateral face with few plumes.

Pleopods (Fig. 1, J–K). Outer ramus 9–13 segmented, inner ramus 6–9 segmented; pleopod 1 peduncle with 8–10 plumes on lateral border, pleopod 3 peduncle with 5–6.

Uropod 1 (Fig. 1, L). Posterior margin of peduncle with 1 seta and 1 stout spine proximally, separated by bare gap from next 2 to 3 marginal spines before 3 large inter-ramal spines. Outer ramus slightly longer than inner, with 9–10 posterior spines; inner ramus with 2–3 marginal spines and about 9 posterior spines.

Uropod 2 (Fig. 1, M). Outer ramus broader and slightly longer than inner; both margins of inner ramus bare.

Uropod 3 (Fig. 1, N). Rami slender, outer slightly longer than inner; terminal article of outer ramus distinctly shorter than peduncle.

Telson (Fig. 1, O). Narrow, with proximal margins nearly parallel; relatively narrow V-cleft extending nearly half-way to base; lobes each with 3 unequal apical spines and a group of 2 spines laterally.

Affinities

P. bousfieldi n. sp. does not show particularly close affinities to either of the two previously described Atlantic species, *P. deichmannae* Bousfield 1965 and *P. wigleyi* Bousfield 1965, but shares certain characters with each, which might suggest that the present species is closest to the ancestral stock from which the others have radiated. It is more similar to *P. deichmannae* in the small number of plumes at the posterior angle of coxae 1, 2, and 3; incised proximal posterior margin of peraeopod 7; small number of mandibular palp comb spines; peraeopod 4 with broad, posteriorly produced coxal plate; pleosome side plate 3 with nearly straight anteroventral margin; and uropod 3 outer ramus with terminal segment distinctly shorter than peduncle. However, it resembles *P. wigleyi* in the shape and spination of peraeopod 7, segment 4; uropod 1 peduncle with spinose posterior margin; peraeopod 6, segment 5 with incised distal margin; and the form of peraeopod 5, segments 4 and 5. *P. bousfieldi* possesses several distinctive characters. The most striking feature of the mouthparts is the reduction of the inner plate of maxilla 1 to a small lobe with only 1 seta. The telson is unique in being narrower and more deeply cleft, and with fewer apical spines, than in the previously described species. Pleosome side plate 3 has fewer lower marginal and lateral facial setae, and both pleopod rami have fewer segments.

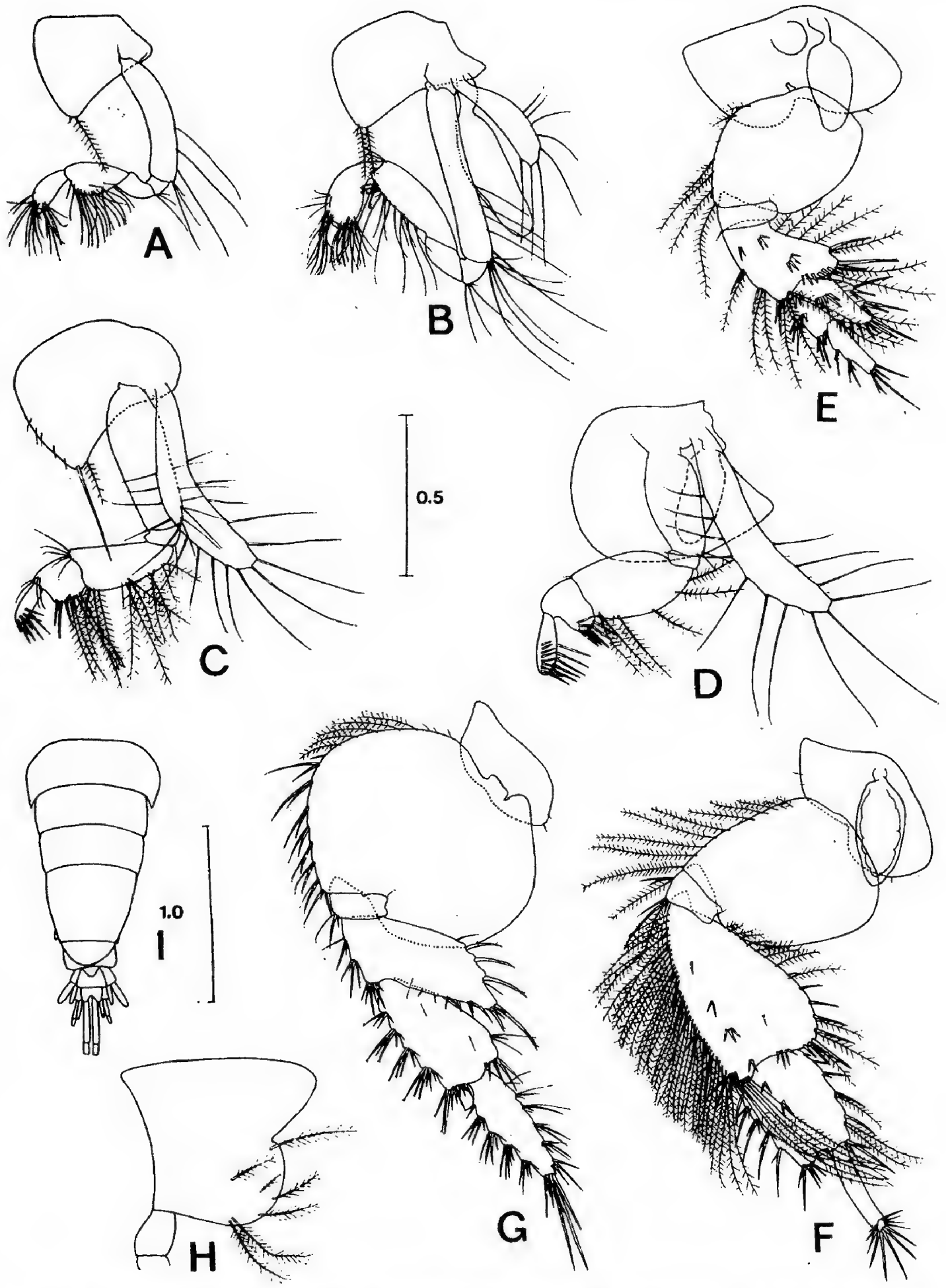

FIG. 2. *Protohaustorius bousfieldi* n. sp., female paratype (ovigerous). A, gnathopod 1; B, gnathopod 2; C, peraeopod 3; D, peraeopod 4; E, peraeopod 5; F, peraepod 6; G, peraeopod 7; H, pleon side plate 3, lateral; I, pleon and urosome, dorsal. Scale lines in mm; A-H, 0.5 mm scale; I as indicated.

The available distribution data suggest that the present new species, like *P. wigleyi* on the Atlantic coast, occupies the shallow subtidal to offshore habitat.

Key to the North American Atlantic and Gulf Species of **Protohaustorius**

1. Peraeopod 7, segment 4 narrowing toward posterior border, with 2 spine groups; uropod 1, posterior margin of peduncle with distal spines only . . . *P. deichmannae* Bousfield 1965. Central Maine south to North Carolina and Georgia, in shallow semi-protected inshore waters and estuaries.

   Peraeopod 7, posterior margin of segment 4 at least as broad as anterior border, with 3–4 spine groups above lower angle; uropod 1, posterior margin of peduncle with spines both proximally and distally. 2

2. Coxa 1, 2, and 3, posterior angle with 4, 7, and 7 plumes respectively; uropod 1, posterior margins of peduncle spinose throughout; mandibular palp, segment 3 with 10 proximal comb spines . . . *P. wigleyi* Bousfield 1965. Central Maine and Georges Bank to off North Carolina, from shoreline to over 80 fathoms.

   Coxa 1, 2, and 3, posterior angle with 1, 2, and 1 plumes respectively; uropod 1, posterior margin of peduncle with 1 proximal spine, separated by gap from following 2 to 3 spines before inter-ramal spines; mandibular palp, segment 3 with 2–4 proximal comb spines . . . *P. bousfieldi* n. sp. Upper Texas coast from Sabine Pass to Point Bolivar, from shoreline to at least 7 meters.

GENERIC CHARACTERIZATION

Genus **Parahaustorius** Bousfield 1965

Body broad. Pleon rounding normally, not overhanging urosome. Head widest posteriorly, rostrum short, acute. Antenna 1, peduncle segment 1 strong; accessory flagellum 2-segmented. Antenna 2, peduncle segment 4 broadly lobate posteriorly.

Mandibular incisor with 1 tooth. Maxilla 1, coxal baler lobe large. Maxilla 2, outer plate broadly expanded. Maxilliped, segment 3 stout, geniculate.

Peraeopods 3 and 4 similar; 3 longer. Peraeopod 7, segment 5, posterior margin long, more than one-half the anterior margin.

Abdominal side plate 3 rounded behind. Uropod 1 strong, normally biramous; inter-ramal spines strong. Uropod 2 strongly biramous. Uropod 3 biramous, slender. Telson broad, moderately cleft. (After Bousfield 1973).

Remarks: The new species agrees with the above diagnosis, except that the head is widest medially.

PARAHAUSTORIUS OBLIQUUS NEW SPECIES

Material Examined

Sea Rim State Park, water depth a few cm to 1 meter, 9 Oct. 1975, PBR and CRS: 9 ♀ ♀ (3 ovig.), length 5.2–6.9 mm, 10 ♂ ♂, 4.2–5.7 mm; High Island,

just south of State Highway 124, water depth 1 meter, 9 Oct. 1975, PBR and CRS: 3 ♀♀ (1 ovig.), 6.3–6.9 mm, 8 ♂♂, 4.3–7.0 mm; southern tip of Bolivar Peninsula, 1–2 km north of jetty, water depth a few cm to 1 meter, 17 Oct. 1975, PBR and CRS: 7 ♀♀ (5 ovig.), 5.1–6.3 mm, 10 ♂♂, 4.0–5.1 mm; southern tip of Galveston Island at San Luis Pass, water depth a few cm to 1 meter, 19 Oct. 1975, S. T. Clark: 12 ♀♀ (9 ovig.), 5.7–7.4 mm, 12 ♂♂, 4.5–6.3 mm; Surfside, water depth 1 meter, 24 May 1976, PBR and CRS: 10 ♂♂, 3.3–4.3 mm, 3 imm.; Mustang Island, Gulf access road #3, water depth 1 meter, 25 May 1976, PBR and CRS: 2 ♀♀, 5.5, 8.0 mm, 2 ♂♂, 4.7, 6.8 mm, 1 imm.; north Padre Island, Malaquite beach, water depth 1.5 m, 25 May 1976, PBR and CRS: 11 ♀♀, 4.3–8.6 mm, 5 ♂♂, 3.8–4.4 mm, 2 imm.

Holotype: Ovigerous female, 6.1 mm, deposited in the U. S. National Museum (USNM 170255).

Paratypes: Female, 5.4 mm, 2 males, 5.0, 5.1 mm, and slides of dissected parts, deposited in the U.S. National Museum (USNM 170256); 2 females, 6.0, 5.4 mm, 2 males, 5.0, 4.9 mm, deposited in the National Museum of Natural Sciences (Canada).

Type locality: Sea Rim State Park, Texas.

Ecology: Clean fine-grained sand on wave-exposed Gulf beaches, from lower intertidal to subtidal depths.

Etymology: The specific name refers to the shallowly oblique posterior margin of segment 4 (merus) of peraeopod 7.

Remarks: This is the largest species of haustoriid amphipod we have collected to date on the Texas coast.

Diagnosis

Head broadest medially. Antenna 1 flagellum 6–7 segmented; accessory flagellum segments unequal. Antenna 2 flagellum 7–8 segmented, first article the longest. Mandibular accessory blades 6–9; palp segment 3 with 10–21 comb spines, apex with 6–7 slender spines. Maxilla 1, inner plate with 9–12 branching setae. Gnathopod 1, posterior coxal angle with 9–15 plumes. Gnathopod 2, posterior coxal angle with 8–11 plumes; segment 5 shorter than 2 and longer than segment 6. Peraeopod 3, coxa semilunate, posterior lobe truncate. Peraeopod 4, coxal plate distinctly longer than broad. Peraeopod 5, coxal lobes shallow, subequal, posterior margin of hind lobe with only a few minute setae. Peraeopod 6, posterior coxal lobe with a few small marginal setae; segment 4 medially broadest, greater than 1.5 times length of segment 5. Peraeopod 7, coxa posterior lobe obtuse; segment 4 subrectangular, posterior margin shallowly oblique rather than sharply truncate, with 2 spines above and 2 stout subequal spines at lower angle. Pleopods, inner ramus with 12–15 segments, outer ramus slightly longer, with 15–20 segments. Uropod 1, posterior margin of peduncle spinose; longest inter-ramal spine greater than one-half the inner ramus. Telson cleft narrowly, half-way to base; lobes smoothly rounding, apically bare, each with 6–7 marginal spine groups.

Description

Male (3.3–7.0 mm) smaller but similar to female (4.3–8.6 mm).

Head (Fig. 3, A). Broadest medially, tapering and rounding posteriorly, rostrum strong, subacute, anterolateral lobes obtuse; eyes present in adults.

Antenna 1 (Fig. 3, B). Flagellum of 6–7 subsequal segments, calceoli slender, 1.5 times length of each segment; accessory segments slender, unequal.

Antenna 2 (Fig. 3, C). Peduncular segment 4 with deep, convex posterior lobe and with short anterior marginal setae; surface sensory setae few; segment 5 tumid, anterior marginal setae short; flagellum 7–8 segmented, basal segment the longest, with posterior plumes.

Upper lip (Fig. 3, E). Broad, apical margin nearly straight, smooth.

Lower lip (Fig. 3, F). Outer lobes large, pilose distally; inner lobes broad, distally short pilose.

Mandible (Fig. 3, D). Incisor simple, lacinia small, unicuspate; 6–9 accessory blades; palp long, slender, segment 3 shorter than 2, with 10–21 short comb spines, apex with 6–7 slender spines.

Maxilla 1 (Fig. 3, G). Inner plate small, with 9–12 branching marginal setae; outer plate broad, with about 16 spine teeth; palp broadest at apex, with simple and plumose setae; accessory lobe large, outer margin shorter than inner.

Maxilla 2 (Fig. 3, H). Outer plate with short inner margin, armed proximally with 16–20 pectinate spines and distally with 16–24 plumes.

Maxilliped (Fig. 3, I). Inner plate with 10 inner marginal plumes and 2 apical teeth; outer plate relatively narrow; palp narrow, distal lobe of segment 2 nearly attaining transverse margin of short, geniculate, distally rounded segment 3.

Gnathopod 1 (Fig. 4, A). Posterior coxal angle rounded, margin with 9–15 plumes; segment 5 elongate, posterior margin heavily setose; segment 6 slender, slightly arched; dactyl small, nail short, apical.

Gnathopod 2 (Fig. 4, B). Posterior coxal angle with 8–11 plumes; segment 2 long and slender; segment 5 shorter than 2 and longer than 6; segment 6 slender, slightly arched, dactyl small, minutely subchelate. Female brood plate with 12–26 distal setae.

Peraeopod 3 (Fig. 4, C). Coxa semilunate, posterior lobe truncate, posterior angle acute, with 7–16 plumes and 3–5 long, naked setae distally; segment 2 powerful, plumose posteriorly; segment 4 broadening distally, margins plumose; segment 5 broad, posterior lobe armed with circlet of 14, occasionally 18, slender spines and 12–20 plumes; segment 6 broad, spatulate, with 14–17 marginal spines. Female brood plate broad, slightly arched, with 40–60 marginal setae.

Peraeopod 4 (Fig. 4, D). Coxal plate distinctly longer than broad, smoothly rounding below, posterior lobe short; segment 2 short, stout, sparsely plumose posteriorly; segment 4 powerful, margins convex and plumose; segment 5 short, deep, lobe circlet with 8–11 spines and 6–8 plumes; segment 6 oval, margin

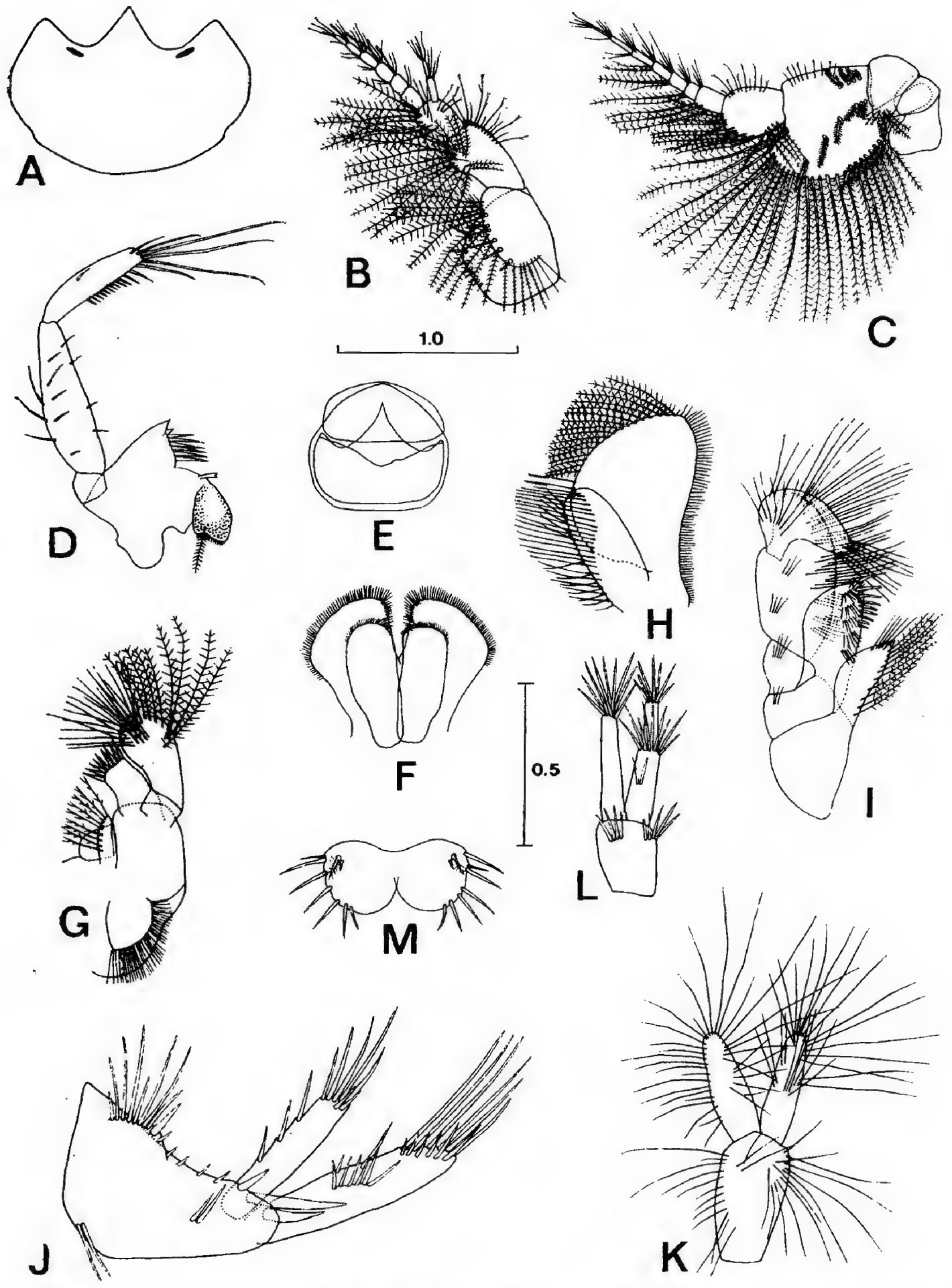

FIG. 3. *Parahaustorius obliquus* n, sp., female paratype (ovigerous). A, head; B, antenna 1; C, antenna 2; D, mandible; E, upper lip; F, lower lip; G, maxilla 1; H, maxilla 2; I, maxilliped; J, uropod 1; K, uropod 2; L, uropod 3; M, telson. Scale lines in mm; A-C same as B; D-M same as L.

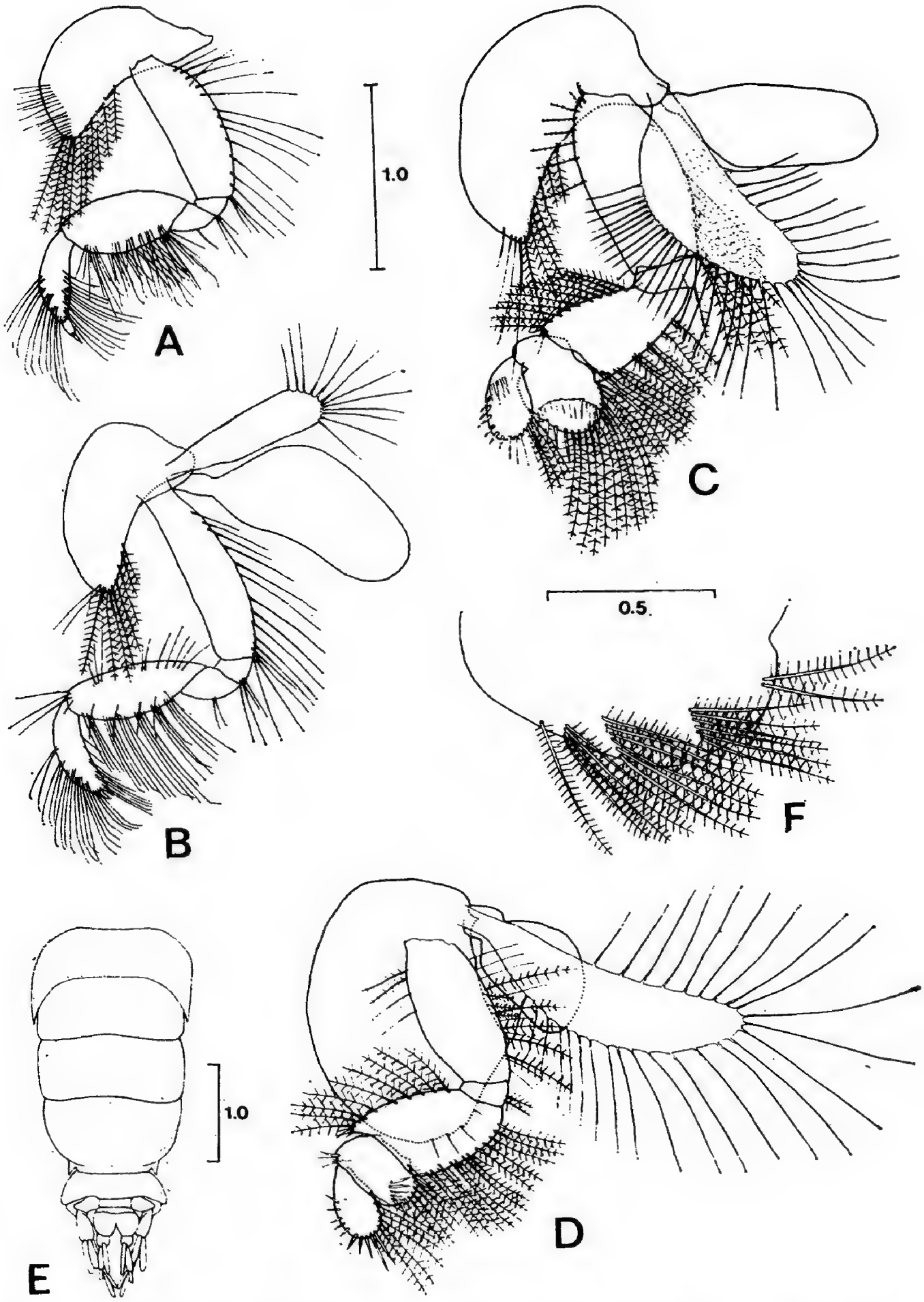

FIG. 4. *Parahaustorius obliquus* n. sp., female paratype (ovigerous). A, gnathopod 1; B, gnathropod 2; C, peraeopod 3; D, peraeopod 4; E, pleon and urosome, dorsal; F, pleon side plate 3, lateral. Scale lines in mm; B-D same as A; E and F as indicated.

nearly ringed with 10–14 spines and 6–9 plumes. Female brood plate long, slightly arched, with 30–40 marginal setae.

Peraeopod 5 (Fig. 5, A). Coxal lobes shallow, subequal, posterior margin of hind lobe with only a few minute setae; segment 2 broader than long, sparsely setose posteriorly; segment 4 wider than long, hind margin with about 5 spine groups and numerous long plumes; segment 5 narrower, with numerous facial spines; segment 6 linear, distinctly longer than segment 5, anterior margin usually with 4 spine groups. Female brood plate short, slender, with 5–7 marginal setae.

Peraeopod 6 (Fig. 5, B). Posterior coxal lobe large, oblique, margin rounded below, with several short setae; segment 2 slightly expanded, narrowing distally, posterior margin bare; segment 4 medially broadest, greater than 1.5 times the length of segment 5, margins subparallel, 4 rows of facial spine clusters, posterior margin with about 10 spines; segment 5 longer than wide, anterior margin narrowing distally; segment 6 about equal to 5, slender, with 4–6 posterior spine clusters.

Peraeopod 7 (Fig. 5, C). Coxa with obtuse posterior lobe; segment 2 broad and orbicular, anterior margin proximally with plumes and distally with spines and plumes, posterior margin nearly bare except for several short proximal setae; segment 4 subrectangular, posterior margin shallowly oblique rather than sharply truncate, with 2 spines above and 2 stout subequal spines at lower angle; segment 5 distally broadest, posterior margin short, with 2–3 spine groups; segment 6 subequal, broadest proximally, with 5–6 spine groups on anterior margin and 6–7 on posterior margin.

Pleosome side plate 3 (Fig. 4, F). Shallowly convex, rounded behind, with 4–6 lateral clusters of 2–8 plumes and 1 anterior singly inserted plume.

Pleopods (Fig. 5, D–E). Peduncle broad, short; pleopod 2 peduncle with 15–20 outer marginal plumes, pleopod 3 peduncle with 9–12 plumes; rami slender, inner 12–15 segmented, outer longer and 15–20 segmented.

Uropod 1 (Fig. 3, J). Peduncle stout, posterior margin lined with 6–8 stout spines, proximal protuberance with 1 strong spine and a row of 7–10 stiff setae; 2 large inter-ramal spines, longer one greater than half the inner ramus; outer ramus longer and heavier than inner, both terminating in a cluster of long spines.

Uropod 2 (Fig. 3, K). Peduncle and rami subequal, with numerous slender simple setae.

Uropod 3 (Fig. 3, L). Rami slender, tapering distally; outer ramus longer, terminal segment shorted than peduncle; inner ramus lacking marginal spines.

Telson (Fig. 3, M). Cleft narrowly, halfway to base, lobes smoothly rounding, apically bare, each with 6–7 marginal spine groups.

Affinities

P. obliquus is closely related to *P. longimerus* Bousfield 1965, which occurs on the Atlantic coast from Cape Cod Bay to northern Florida. However, *P.*

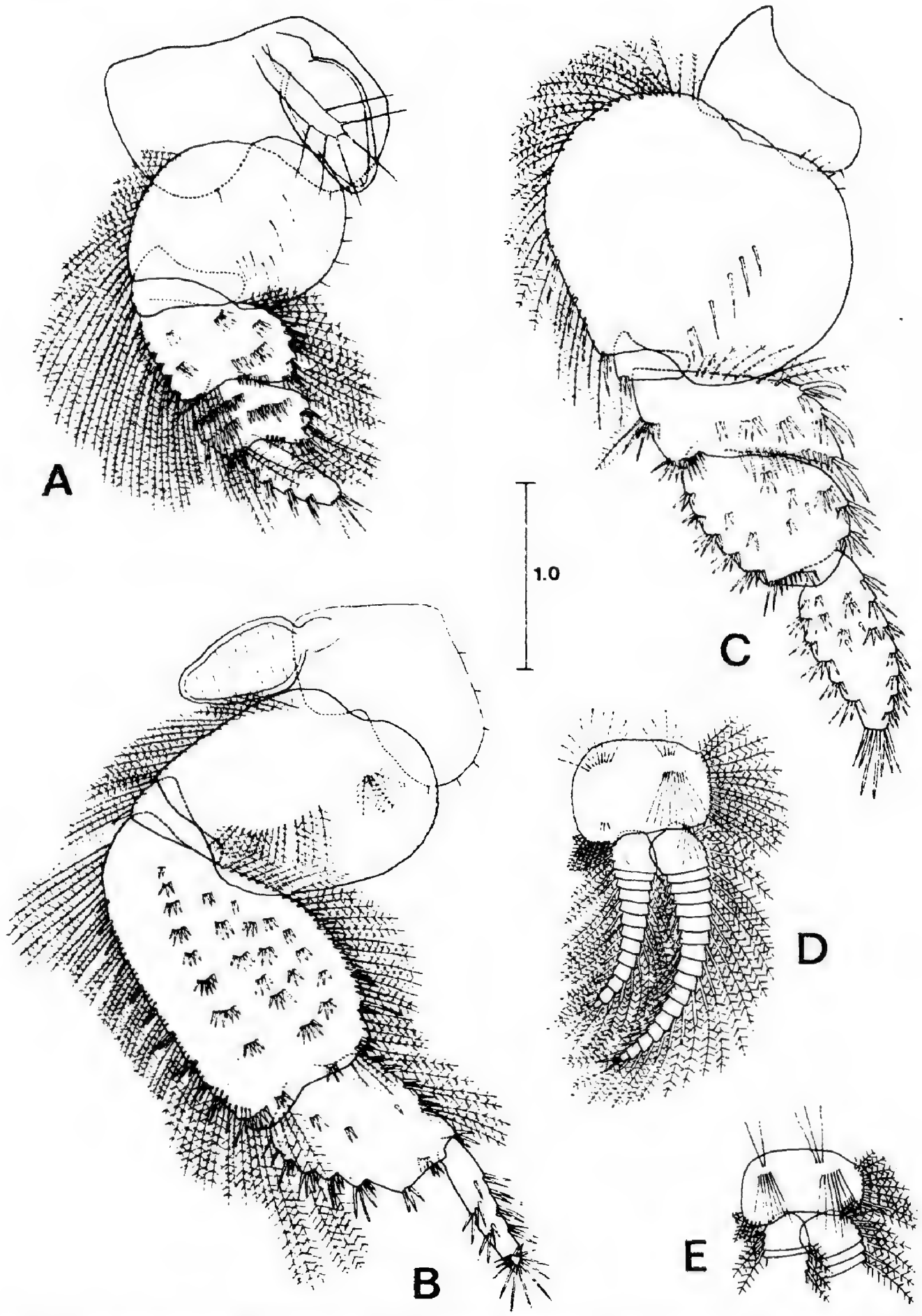

FIG. 5. *Parahaustorius obliquus* n. sp., female paratype (ovigerous). A, peraeopod 5; B, peraeopod 6; C, peraeopod 7; D, pleopod 2; E, pleopod 3, peduncle. Scale line in mm.

obliquus is smaller (3.3–8.6 mm compared to 7–10 mm for *P. longimerus*) and is distinctly different in the following characters: head broadest medially; both antennal flagella with fewer segments; mandibular palp segment 3 with fewer

comb spines; peraeopod 4, coxal plate longer than broad; peraeopod 7, segment 4 posterior margin shallowly oblique rather than sharply truncate, with 2 stout subequal spines at lower angle; both pleopod rami with fewer segments; and uropod 1, larger inter-ramal spine greater than one-half length of inner ramus. There are also differences in the number of spines and setae on various appendages.

The available distribution data indicate that the habitat of the present species is similar to that of *P. longimerus* on the Atlantic coast.

Key to the North American Atlantic and Gulf Species of **Parahaustorius**

1. Peraeopod 7, coxal plate broadly acute or obtuse behind; segment 6 about equal to 5; uropod 1, posterior margin of peduncle spinose throughout; telson narrowly cleft, lobes rounded. 2

   Peraeopod 7, coxal plate sharply elongated behind; segment 6 distinctly longer than 5; uropod 1, posterior margin of peduncle centrally unarmed; telson very broad, shallowly V-cleft . . . *P. attenuatus* Bousfield 1965. Georges Bank and off Cape Cod south to mouth of Chesapeake Bay.

2. Peraeopod 7, segment 4 narrowing behind, posterior margin oblique, with 1 stout spine; peraeopod 6, segment 4 lightly longer than 5, broadening distally . . . *P. holmesi* Bousfield 1965. Georges Bank and off Cape Cod south to mouth of Chesapeake Bay.

   Peraeopod 7, segment 4 subrectangular, with 2 (or 3) stout spines above lower angle; peraeopod 6, segment 4 at least 1.5 times longer than 5, medially broadest. 3

3. Peraeopod 7, segment 4 posterior margin sharply truncate, with 1 stout spine at lower angle; mandibular palp, segment 3 with about 30 comb spines; uropod 1, inter-ramal spines less than one-half length of inner ramus . . . *P. longimerus* Bousfield 1965. Georges Bank and Cape Cod south to Cape Kennedy, Florida.

   Peraeopod 7, segment 4 posterior margin shallowly oblique, with 2 stout subequal spines at lower angle; mandibular palp, segment 3 with 10–21 comb spines; uropod 1, larger inter-ramal spine greater than one-half length of inner ramus . . . *P. obliquus* n. sp. Texas coast from Sea Rim State Park to north Padre Island.

LITERATURE CITED

BOUSFIELD, E. L. 1965. The Haustoriidae of New England (Crustacea: Amphipoda). *Proc. U. S. Nat. Museum.* **117** (3512):159–240.

————. 1970. Adaptive radiation in sand-burrowing amphipod crustaceans. *Chesapeake Sci.* **11**(3):143–154.

————. 1973. *Shallow-water gammaridean Amphipoda of New England.* Cornell Univ. Press, Ithaca, N.Y., 312 pp.

CROKER, R. A. 1967. Niche diversity in five sympatric species of intertidal amphipods (Crustacea: Haustoriidae). *Ecol. Monogr.* **37**(3):173–198.

DEXTER, D. M. 1967. Distribution and niche diversity of haustoriid amphipods in North Carolina. *Chesapeake Sci.* **8**(3):187–192.

————. 1971. Life history of the sandy-beach amphipod *Neohaustorius schmitzi* (Crustacea: Haustoriidae). *Mar Biol.* **8**:232–237.

HOLLAND, A. F. and T. T. POLGAR. 1976. Seasonal changes in the structure of an intertidal community. *Mar. Biol.* **37**:341–348.

HOWARD, J. D. and C. A. ELDERS. 1970. Burrowing patterns of haustoriid amphipods from Sapelo Island, Georgia. In: *Trace fossils*, pp. 243–261. Ed. by T. P. Grimes and J. C. Harper. Geol. Jour. Special Issue No. 3. Liverpool, Seel House Press.

IVESTER, M. S. and B. C. COULL. 1975. Comparative study of ultrastructural morphology of some mouthparts of four haustoriid amphipods. *Can. J. Zool.* **53**:408–417.

SAMEOTO, D. D. 1969. Comparative ecology, life histories, and behaviour of intertidal sand-burrowing amphipods (Crustacea: Haustoriidae) at Cape Cod. *J. Fish. Res. Bd. Canada.* **26**: 361–388.

THE FEASIBILITY OF SUSPENSION CULTURE OF OYSTERS (*CRASSOSTREA VIRGINICA*) AT A PETROLEUM PLATFORM OFF THE TEXAS COAST[1]

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ABSTRACT

The feasibility of experimental off-bottom oyster culture at a petroleum platform offshore from High Island, Texas was established. Growth was compared to that of an oyster population which was held in the estuary in the Galveston Ship Channel at Pelican Island, Galveston. Offshore and estuarine oysters (120 of each group ranging from 42 to 87 mm length) were suspended at two levels in plastic mesh "Vexar" bags. The rate of growth of oysters in terms of length was not significantly different for depth or for station. The rate of growth in terms of weight was significantly greater for the estuarine oysters due to a significantly greater rate of growth for oysters at the lower level of that station. The condition index of oysters was higher at the estuarine station than offshore. The chlorophyll *a* level in the estuary was twice that offshore, indicating a denser phytoplankton standing crop. However, generic composition of the phytoplankton was similar in both stations. Mortality was greater offshore (51 of 120) than at the estuarine station (32 of 120) and was possibly related to the greater incidence of the fungus *Labyrinthomyxa marina* in the offshore oysters. The problems of adequately containing oysters, obtaining spat and securing disease free oysters must be dealt with before an adequate assessment can be made for using petroleum platforms to culture oysters offshore.

INTRODUCTION

The presence of a large number of petroleum platforms offshore from Louisiana and Texas provide potential stationary structures for suspension culture of oysters. Moreover, the increased demand for domestic petroleum resources makes it likely that the number of platforms will be greatly increased in the near future. The useful life of offshore platforms might be extended beyond the time required to deplete the oil resources in the area by providing subsequent alternate uses such as oyster mariculture for such platforms.

[1] Based in part on a thesis submitted to the Faculty of the Graduate School of Texas A&M University by John Ogle in partial fulfillment of the requirements for the degree of Master of Science, May, 1975.

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There are no major populations of oysters (used here to refer exclusively to *Crassostrea virginica*) in the high salinity waters of the Gulf of Mexico (Price 1954, Dawson 1955). Oysters are known to tolerate salinities from 10–34 ppt (Galtsoff 1964). They are also known to occur naturally offshore on oil platforms (Gunter 1951, Gunter and Geyer 1955). The action of predators (Menzel, Hulings and Hathaway 1958; Wells and Gray 1960) and diseases (Ray and Chandler 1955) have been proposed as an explanation for the absence of major oyster populations in waters of high (oceanic) salinities. Fish predators could be excluded by holding oysters in bags. Adult benthic predators, could be eliminted by suspending oysters freely away from contact with the platform's supports. The southern oyster drill (*Thais haemostoma*) which has planktonic larvae (St. Amant 1938) might present a problem, especially as they occur in great numbers in high salinity and offshore areas. The problems to be expected from disease, primarily the fungus parasite *Labyrinthomyxa marina* (Mackin, Owen and Collier 1950; Mackin and Ray 1966) (=*Dermocystidium marinum*) are not known. A similar mortality rate has been found in infected oysters suspended offshore as compared to oysters suspended in the bay (Ray, unpublished data). Assuming that the focus of infection is in the bay, it is probable that oysters free from the fungus would remain so when placed offshore.

MATERIALS AND METHODS

Description of the Study Area

The area in which studies were conducted lies southeast of Houston, Texas, in the northwest Gulf of Mexico. The Atlantic Richfield Company (ARCO) allowed an experimental station to be established at platform B, located six kilometers offshore from High Island, Texas (Fig. 1) in approximately 10 meters of water. Prevailing currents were from the east and wave heights of less than one meter to two meters were recorded during 12 monthly observations. The platform, is fully automated and is inhabited only during the day. Transportation by helicopter from the land base to the platform was provided by ARCO.

For comparison a second station was established in Galveston Channel at Pelican Island at a pier on the Moody College of Marine Sciences Campus (Fig. 1). This site was selected because the campus is patrolled by security personnel, giving some degree of protection from vandalism. The station is exposed to ship traffic and industrial and municipal pollution, but is sheltered from wave action for nine months of the year because of the presence of the vessel TEXAS CLIPPER at the pier. The water depth at the pier is approximately five meters.

Plastic mesh bags were used to hold the young adult oysters and were made from 60 cm lengths of 2 cm mesh plastic "Vexar" tubular bagging. A chain shackled to a cable was passed through the center of the bag. A 30 cm length of brass brazing rod was passed through the bag and through a link in the chain. Both ends of the pin were bent to prevent its loss. The bags were folded in the center in a "saddlebag" fashion, and contained a total of 20 oysters, 10 on each side. Both open ends were closed at the bottom by passing a 30 cm length of braz-

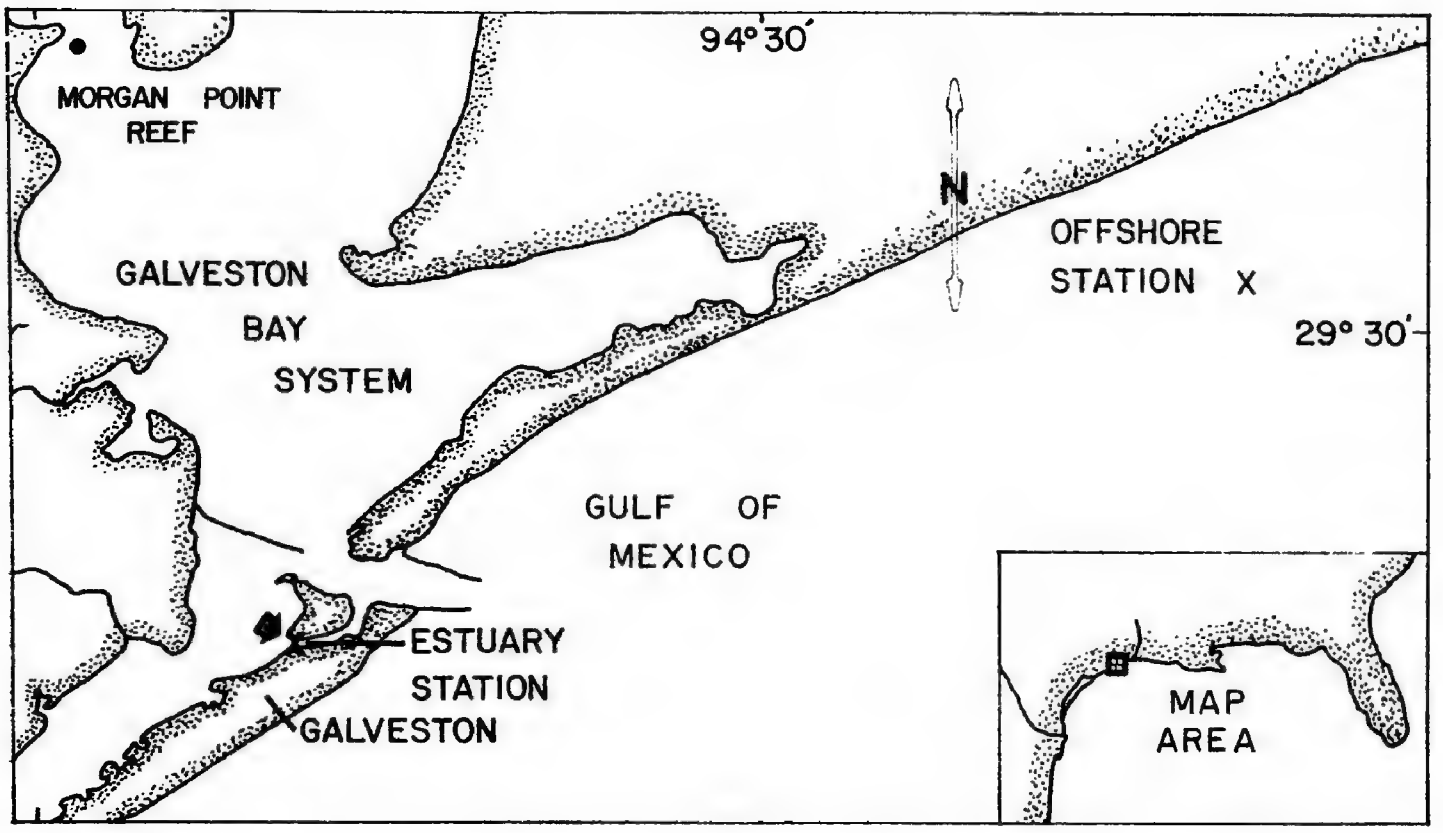

FIG. 1. Location of the two stations in the Northwest Gulf of Mexico along the Texas Coast.

ing rod through the mesh and the supporting chain. The two bottom pins were bent on one end only to allow their removal for access to the bag (Fig. 2). Each bag was subdivided to contain 5 oysters, by the use of an additional pin, thus securing the oysters so that shifts in their position would be minimal.

Six "saddlebags" (12 bags) were positioned in each of two groups spaced 1 m apart along a length of 25 mm stainless steel cable to which the chain was attached. Offshore, this cable was attached to a main support cable of 127 mm stainless steel wound onto a Beebe #10 winch (800 kg capacity) installed in the center of the upper deck of the platform (Fig. 3). Two additional lengths of cable containing bags of oysters from another experiment were also attached to the main support cable. Three 1.8 m lengths of 2.5 cm galvanized pipe equally spaced along the cable were used to spread the three cables apart.

The entire support apparatus was positioned centrally under the platform by means of stainless steel 64 mm tether cables attached to the platform at three points. The apparatus was lowered into the water and positioned so that the top bags were 2 meters from the surface at mean low water and the bottom bags were 6 m from the surface and approximately 4 m off the bottom. Such positioning of the oyster reduced the effect of wave action and excluded benthic predators.

At the estuary station "saddlebags" were pinned along a length of stainless steel chain attached to the hand railing of the pier and positioned to extend to within ½ meter of the bottom. No saddlebags were within ½ meter of the surface at mean low water (Fig. 3).

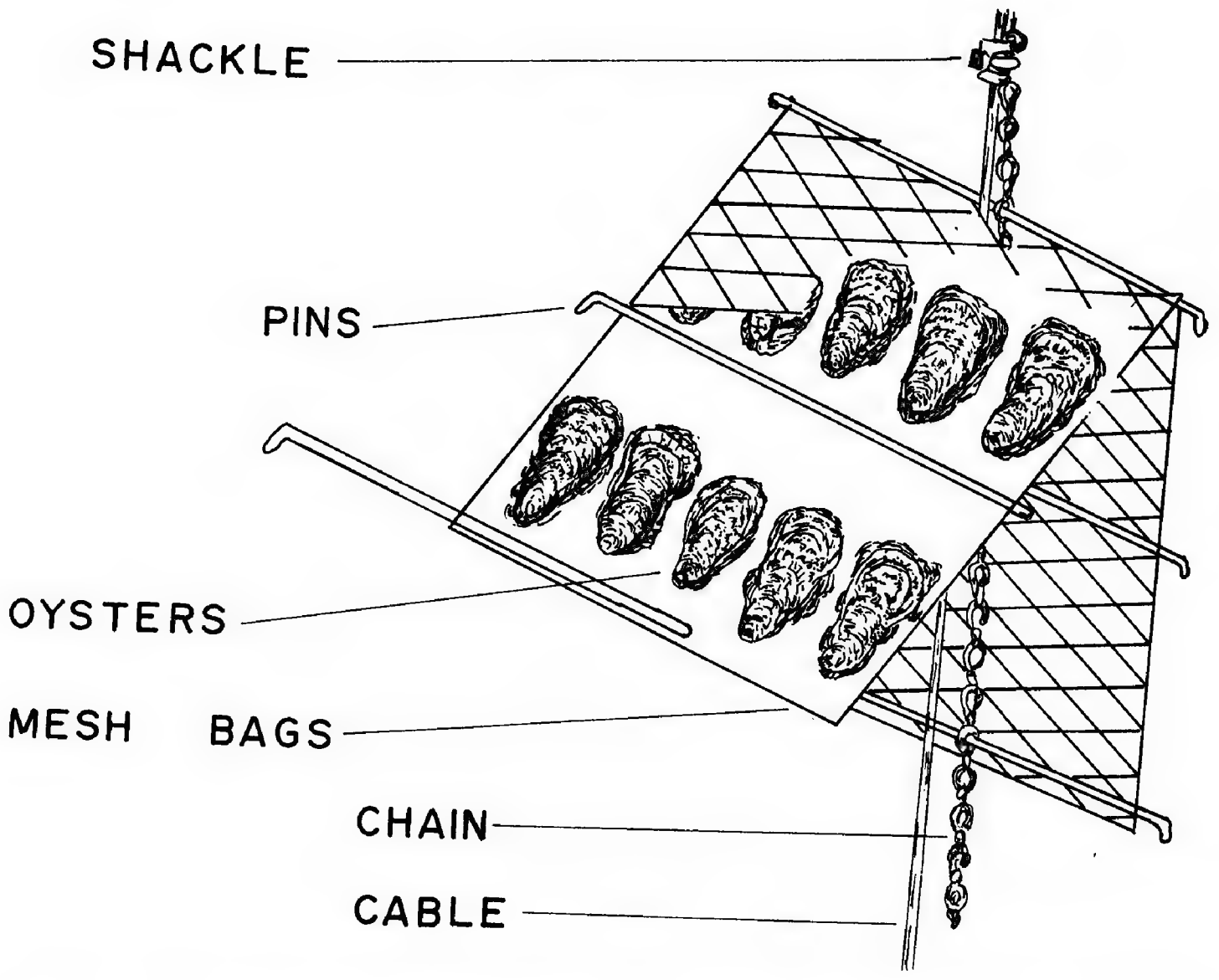

FIG 2. Method for Containment of Oysters in Saddlebags and Placement of Bags on a Cable.

Collection and Preparation

Oysters were dredged from a reef on a spoil bank adjacent to the Houston Ship Channel in the vicinity of Morgan Point, near Houston, Texas during October 1973. They were culled into singles and cleaned of all superficial fouling organisms with a wire brush. Oysters were placed at both stations on October 23, 1973 and the experiment was terminated one year later on October 23, 1974.

To ensure uniformity in size, the population of oysters was first separated into six size groups (ranging from 40–49 to 90–99 mm in length). Length was taken as the greatest distance from the umbo to the posterior extremity of the shell (measured to the nearest mm). These six size groups were then used to form four groups of 120 oysters having nearly equal length ($\bar{x}$ 67 mm). Oysters in each of the four groups were separated into groups of 10 oysters having nearly equal biomass (840g ± 40g).

Oysters were cleaned of fouling organisms and placed in open containers to dry for 2–3 hours. The weight of individual oysters were determined to the nearest gram by weighing in air on a 1000-g capacity Sartorius balance and recorded along with the length and position of the oyster in a bag.

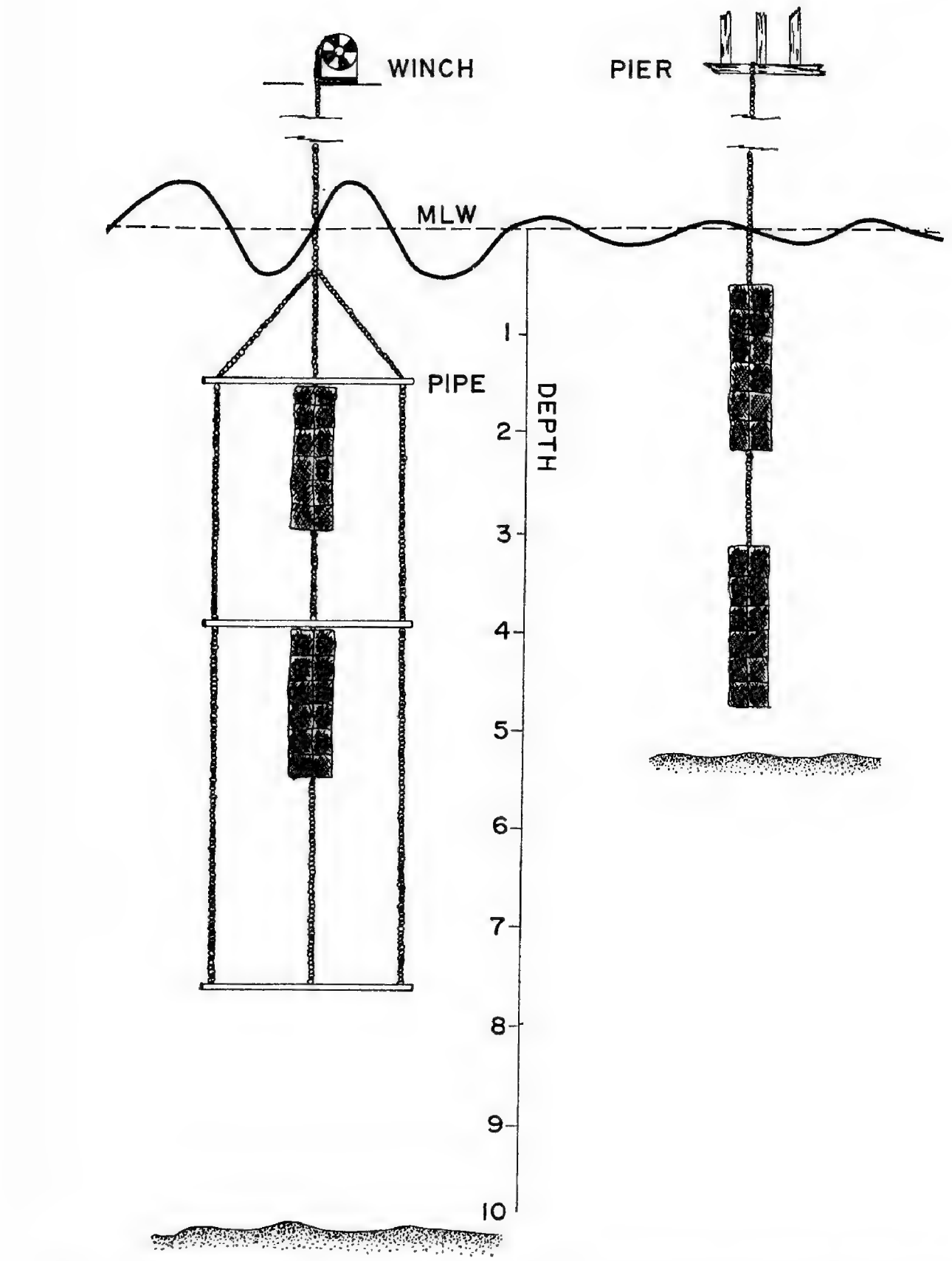

FIG. 3. Method for Placement of Saddlebags on Support Apparatus at Both Stations. Depth in Meters from Surface at Mean Low Water (MLW).

Sampling Procedure

Every 2 months, one intact bag containing (initially) 10 oysters (including both live and dead animals) was removed from both levels at both stations. Mortalities were noted and changes in length and live weight were determined for each oyster. The monthly rate of growth in terms of length and weight, calculated

for each individual was used in obtaining averages for each sampling interval and for the entire study. Analysis of variance was used to test for the effects of stations and the effect of depth at each station on the rate of growth.

Level of infection by the parasite *Labyrinthomyxa marina* was determined according to the technique of Ray (1952 and 1966). A single piece of the anterior mantle was placed in fluid thioglycollate fortified with antibiotics (mycostatin and chloromycetin) and cultured for 7 days. After culture the tissue was blotted dry, teased apart, stained with Lugol's Iodine, examined microscopically at 100X, and rated for infection intensity according to the procedure of Ray (1954). The weighted incidence was calculated according to the procedure of Mackin (1962).

An average condition index (CI) was calculated for oysters according to the equation of Hopkins (1949) as follows:

$$\text{CI} = \frac{\text{mean dry meat weight in grams}}{\text{shell cavity volume in milliliters}} \times 100$$

The volume of the shells was determined by water displacement (Galtsoff 1964). The difference between the displacement of the live closed oyster and the displacement of the detached shells after removing the oyster meat was taken to be the volume of the shell cavity. Dry meat weight was determined by drying the oyster meats to a constant weight ($\pm$ 0.01g) at 100°C in tared aluminum pans.

Bags with oysters missing were eliminated from the study. However the bags were not removed from the chain, in order to preserve the sequence of the bags for accounting.

Surface (1 m from surface) and bottom (8 m from surface offshore, 5 m from surface in the estuary) water samples were taken with a 250-ml subsurface water sample (constructed of clear plastic tubing and closed by two rubber balls) for the determination of several hydrographic parameters.

Temperature was determined with a mercury thermometer to the nearest degree Celsius at the time of collection. A Ryan 45-day continuous temperature recorder was placed at the offshore station (in March 1973) at a depth of approximately 5 meters. The instrument was checked monthly and calibrated to the temperature of a water sample collected from 5 meters. A continuous record of the water temperature was obtained for 9 of the 12 months of this study. Use of a similar instrument suspended at the estuarine station was abandoned due to apparent tampering with the instrument.

Salinity of the samples were determined to the nearest ppt with a refractometer (Goldberg type, total solids Meter, AO, precision $\pm$ 0.5 ppt).

Surface and bottom water samples for both stations were analyzed for chlorophyll *a* content and the generic composition of the phytoplankton was noted. Water samples were place in 150-ml bottles and transported to the lab in the dark. In the laboratory, samples were refrigerated (ca. 4°C) and the analysis was conducted within 8 hours of the time of collection for both stations.

A well mixed, 10-ml aliquot of the water sample was extracted according to the procedure of Strickland and Parsons (1968) for chlorophyll *a* determinations. The fluorescence was determined on a Turner Model III Fluorometer having a

door modified for 16 × 125 mm tubes and a C–2–60 filter and the chlorophyll a content of the water was calculated in milligrams per cubic meter of seawater.

The generic composition of the live phytoplankton was determined by microscopic examination of centrifuged samples. Because 10 ml samples provided few cells, five lots of 10 ml each, a total of 50 ml were centrifuged for each sample. One drop of the concentrate was examined on a slide at 100X. All fields of the slide were examined and the phytoplankton cells present were identified to genus. Visual estimates were made to determine the numerically dominant genus or genera.

RESULTS

Growth and Survival

The average initial lengths and weights and the calculated growth rates of oysters surviving in each of six bags after intervals of 2, 4, 6, 8, 10 and 12 months from the start of the experiment are presented in Table 1. The monthly rate of growth in terms of length (2.6 mm/Mo offshore vs. 2.9 mm/Mo in the estuary) combined from the 6 samples and the 2 depths for each station were not significantly different ($P > 0.5$, Table 2) between stations. The rate of growth in terms of weight was significantly ($P < 0.5$, Table 2) greater at the estuarine station

TABLE 1

Initial size, rate of growth, and condition index (C.I.) for oysters suspended at two locations at two depths along the Texas Coast.

Offshore Upper Level

Duration Months	Number	C.I.	Initial Size mm	Initial Size g	Growth Rate mm/Mo	Growth Rate g/Mo
2	9	6.6	67	79.24	2.6	7.10
4	7	6.5	67	85.63	2.9	5.60
6	8	11.6	68	73.20	2.3	6.12
8	5	13.6	76	98.13	1.6	7.42
10	4	4.2	70	85.46	1.5	4.78
12	4	4.8	68	90.20	1.3	6.12
			Mean		2.2	6.29
			Variance		2.07	10.51

Estuary Upper Level

Duration Months	Number	C.I.	Initial Size mm	Initial Size g	Growth Rate mm/Mo	Growth Rate g/Mo
2	7	10.0	68	85.13	4.6	9.93
4	9	8.9	64	76.59	2.6	7.26
6	9	11.1	63	72.09	2.5	6.47
8	7	12.4	70	82.87	2.3	5.83
10	6	7.5	68	80.37	2.1	7.63
12	7	9.2	68	84.96	1.9	6.85
			Mean		2.7	6.50
			Variance		1.99	12.44

Offshore Lower Level

Duration Months	Number	C.I.	Initial Size mm	Initial Size g	Growth Rate mm/Mo	Growth Rate g/Mo
2	8	5.0	66	86.46	4.3	6.69
4	9	6.6	66	87.30	3.1	6.93
6	1	0.4	59	65.73	0.7	1.46
8	7	10.9	68	91.67	2.9	6.47
10	5	5.2	72	87.70	2.7	7.58
12	1	2.4	70	82.47	1.4	2.96
			Mean		3.1	6.57
			Variance		2.89	6.34

Estuary Lower Level

Duration Months	Number	C.I.	Initial Size mm	Initial Size g	Growth Rate mm/Mo	Growth Rate g/Mo
2	10	8.3	67	87.50	3.4	8.64
4	9	9.6	66	80.23	3.8	10.62
6	7	9.4	68	81.28	3.3	11.66
8	9	8.9	67	88.09	3.4	10.37
10	6	6.8	59	90.96	1.8	7.54
12	2	5.8	72	91.56	1.6	6.68
			Mean		3.2	9.41
			Variance		2.05	16.03

For Both Levels Combined

			Mean		2.6	6.4
			Variance		2.61	8.61
			Mean		2.9	8.4
			Variance		2.11	12.51

(8.44 g/Mo) than at the offshore station (6.42 g/Mo) due to the significantly greater rate of growth (9.41 g/Mo) for oysters at the lower level than for oysters suspended at the surface in the estuary (6.50 g/Mo). There was no significant difference in rate of growth between levels offshore.

Oyster mortality was greater offshore (data taken from Table 1), with 51 deaths out of 120 oysters (both levels combined) than in the estuary with 32 deaths out of 120 oysters (both levels combined). In only two sampling periods did all oysters survive: offshore after four months and at the estuary after two months. Only one oyster survived in bags sampled during April and October 1974 offshore while only two oysters remained in a bag sampled from the estuary in October 1974.

Despite the attempt to secure disease-free oysters, incidence (I) and weighted incidence (W.I.) of the fungus parasite, *L. marina*, in oysters at both study areas was greater than for oysters at the collecting site (Fig. 4). The Morgan Point reef was sampled initially in September 1973 (15 oysters) and the parasite was not found. In October 1973, when oysters were collected, 3 of 24 oysters assayed showed a low level of infection (W.I., O.I., I., 13%). A check of 10 oysters from the reefs in December 1973 failed to detect the parasite but a final check of 25 oysters in April 1974 revealed that the parasite was present at a higher level than previously detected (W.I., 0.3; I., 28%). Fungus infections in oysters in this study exceeded the level of infection for oysters from the natural reef (W.I., 0.1; I., 12%) in all but one sample of seven oysters (lower level, estuarine station, April 1974). Oysters offshore generally had a greater infection than oysters in the estuary.

Condition Index (C. I.)

The seasonal variation in C.I. (Table 1) for oysters offshore (from 13.6 to 4.2 upper level; from 10.9 to 0.4 lower level) was greater than for oysters in the estuary (from 12.4 to 7.5 upper level; from 9.6 to 5.8 lower level). The C.I. was generally highest during April and June for both stations but was higher in the

TABLE 2

F values of oyster growth for two depths and two stations along the Texas Coast.

Source of Variation	Length	Weight
Depth (Offshore)	5.88	0.15
Depth (Estuary)	2.82	12.92*
Station (Depths Combined)	1.42	14.41*

*Significant ($P < 0.5$)

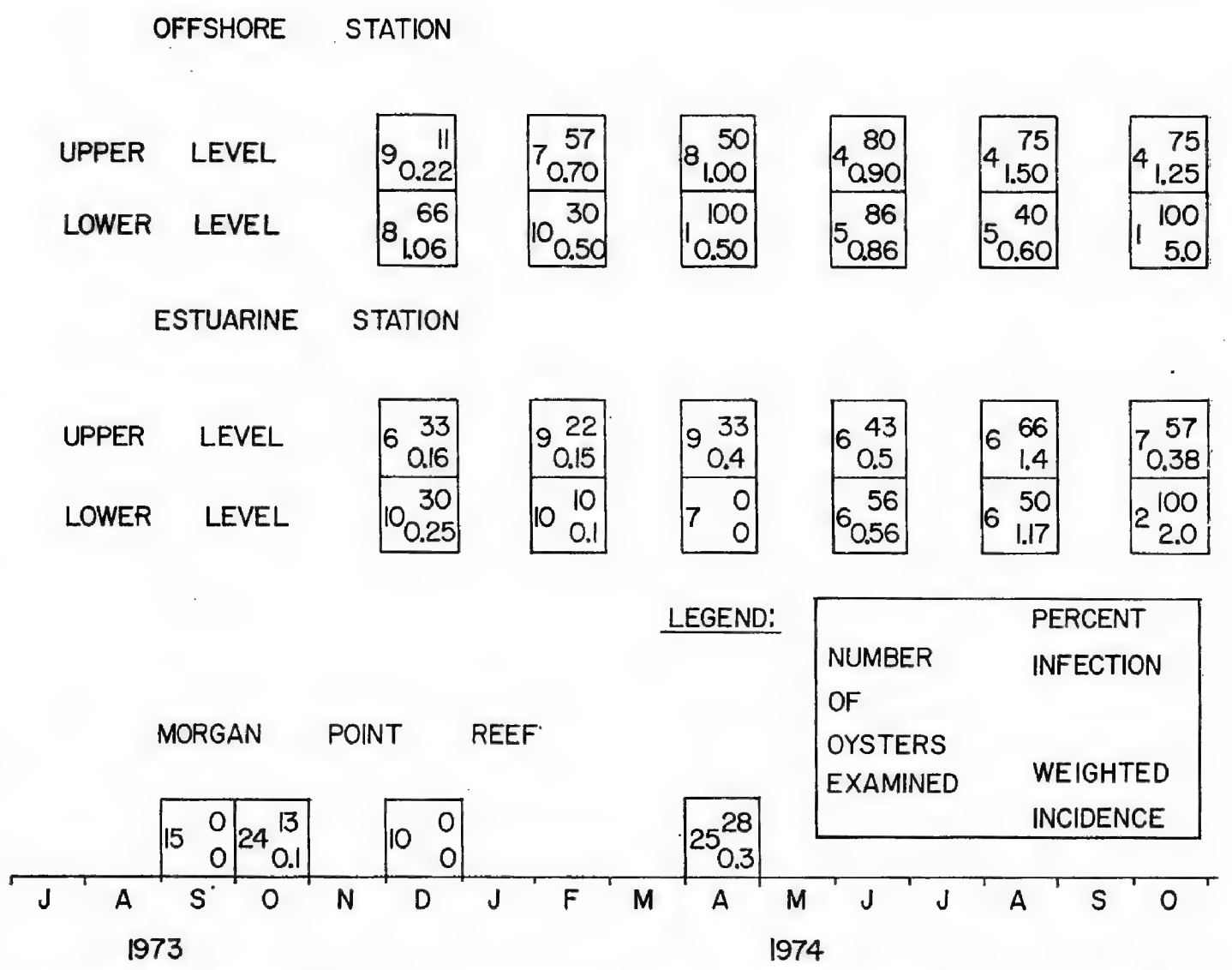

FIG. 4. Incidence of Infection by *Labyrinthomyxa marina* in Oysters From a Natural Reef and for Oysters Suspended at Two Locations at the Two Depths along the Texas Coast.

estuary than offshore (by as much as 9.0 or as little as 0.5) in all but one month (June, 1974).

Hydrographic Data

Temperature data (Figure 5), obtained for 272 days of the 13-month (October 1973–October 1974) study indicate that the offshore water temperature changed

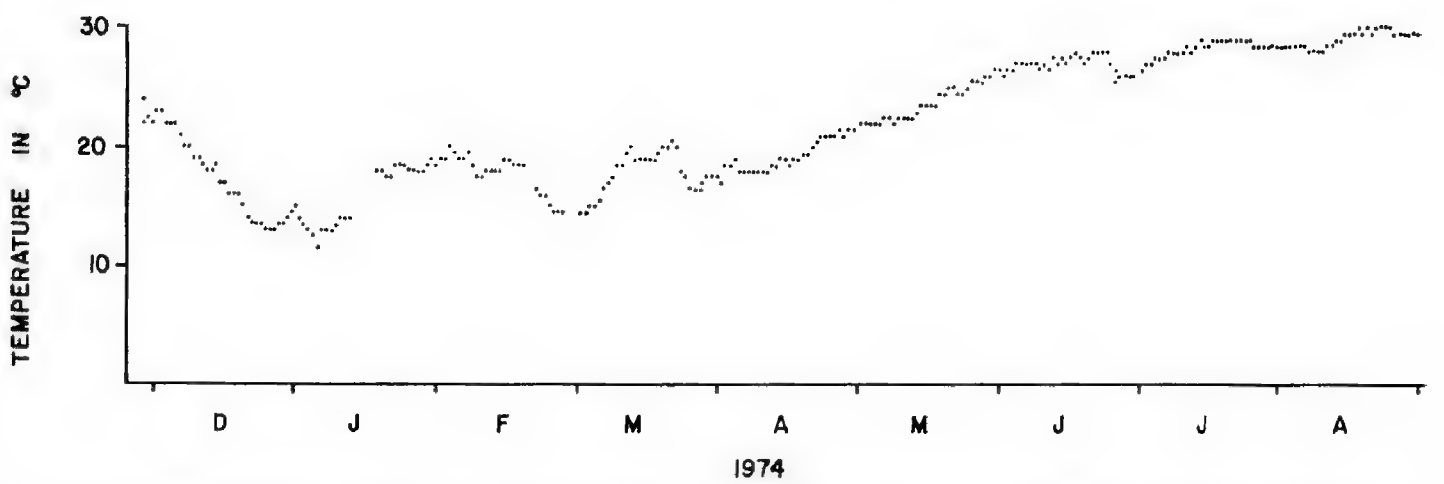

FIG. 5. Daily Water Temperature (°C) at a Mid-depth from the Offshore Station Along the Texas Coast.

slowly varying more than 1°C from one day to the next only during the month of March 1974. Thus the monthly values (Table 3) are probably representative of true trends in temperature. The highest temperature was recorded during July 1974 (30°C at the estuary and 29°C offshore) and the lowest temperature (14°C at both stations) was recorded during February 1974. The temperature never varied more than 2°C between levels at either station nor more than 3°C between stations during a month.

The average salinity was similar at both stations (Table 3) averaging 25 ppt offshore (from 32 ppt to 16 ppt) and 21 ppt in the estuary (from 28 ppt to 16 ppt). Salinities differed between stations by as much as 13 ppt (October 1973) or as little as 1 ppt (April 1974, August 1974 and October 1974).

The average chlorophyll *a* content (Table 3) of the estuarine water (8.2 mg/m³ surface and 7.9 mg/m³ bottom) was generally greater than for the offshore water (4.5 mg/m³ surface and 3.4 mg/m³ bottom). The offshore chlorophyll *a* content of the water varied from 11.4 mg/m³ to 0.7 mg/m³ while in the

TABLE 3

Temperature in °C, Salinity in ppt and Chlorophyll *a* in mg/m³ Determined at Two Depths from Each of Two Stations over 13 Months.

		1973					1974								
		Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Average
Temperature °C															
Offshore	S	24	24	19	20	16	17	21	26	27	29	27	24	11	24
	B	26	24	18	18	16	19	20	26	27	29	28	25	22	23
Estuary	S	24	23	18	18	15	18	20	27	29	30	29	24	23	23
	B	24	24	18	18	16	19	20	27	28	30	29	25	23	23
Salinity %															
Offshore	S	23	29	26	16	28	21	18	22	25	32	26	24	25	24
	B	29	30	27	24	28	21	22	25	28	30	28	24	25	26
Estuary	S	15	18	21	18	16	24	18	18	22	28	28	20	24	21
	B	16	19	24	18	18	26	18	22	26	28	28	20	24	21
Chlorophyll-a mg/m^3															
Offshore	S	3.7	0.7	5.2	8.4	5.6	4.3	5.6	4.9	11.4	1.6	2.6	3.7	1.6	4.5
	B	1.1	0.7	4.9	5.1	5.9	4.5	5.9	2.4	5.7	1.9	1.6	3.8	1.7	3.4
Estuary	S	9.5	4.3	4.8	6.1	5.6	5.9	6.1	5.9	11.7	12.0	14.2	12.0	8.1	8.2
	B	5.0	4.1	3.2	4.5	7.8	4.6	5.6	3.2	13.4	12.6	18.2	12.3	7.8	7.9

S = 1m from surface at both stations

B = 8m from surface offshore, 5m from surface in the estuary

estuary the chlorophyll *a* content of the water varied from 18 mg/m³ to 3.2 mg/m³.

Thirty-two phytoplankton genera were recognized, including 1 euglenoid, 1 chlorophyte, 6 flagellates, 3 silicoflagellates and 21 diatoms (Table 4). Twenty genera were common to both stations. Six genera were unique to each of the stations. At the offshore station, diversity was greatest in September (10 genera present) and least during November (1 genus present) while in the estuary, diversity was greatest in August (12 genera present) and least during October 1973 (2 genera present). *Thalassiosira* and *Coscinodiscus* were the two most frequent dominants for both stations.

DISCUSSION

The greatest rate of weight gain of oysters in the estuarine station may be related to the greater amount of chlorophyll *a*, indicative of the quantity of phytoplankton present in the water. This abundance of phytoplankton was probably due to the presence of a municipal treatment plant in the vicinity of the estuarine station. The generic composition of the phytoplankton was similar at the two stations (20 of 32 common genera). Temperature did not differ sufficiently between stations to account for differences in growth. The greater average salinity offshore (25 ppt vs 21 ppt) is also probably not sufficient to explain the weight differences between the two groups of oysters. The rate of growth in terms of length in this study (2.6 mm/Mo offshore, 2.9 mm/Mo in the estuary) was comparable with what would be expected for oysters from reefs in Galveston Bay. Hofstetter, Hefferson and King (1965) reported on comparative growth studies from two reefs in Galveston Bay for 2 years (1963 and 1965). Growth of oysters in trays from Switchover Reef (an artificial reef) during 8 months (May–December) was 3.7 mm per month during 1963 and 1.4 mm per month during 1965. Oysters from Hanna's Reef (a natural reef) grew 0.5 mm per month during 1963 and 1.9 mm per month during 1965.

The greater condition index for oysters at the estuarine station and the smaller range in values over the year as opposed to the offshore station was probably due to the greater abundance of food and less agitation from wave action in the estuary. The attainment of best condition during April and June in this study suggests that the oysters did not spawn. The single oyster from the lower level offshore sampled during April is probably not representative as indicated by its poor growth.

The greater number of deaths (51 of 120) offshore compared to the estuary (32 of 120) was possibly related to the greater incidence of the fungus *L. marina* observed in the oysters offshore. The level of infection noted for oysters from the low salinity estuarine site of collection was generally exceeded in the oysters suspended at both stations. The fungus may have spread due to the high salinity and the close proximity of bags.

Predators were successfully excluded from the bags and did not present a major problem. Both the flatworm (*Stylochus*) and the southern oyster drill

TABLE 4

Genera of Phytoplankton Present in Water Samples From the Two Stations in the Northwest Gulf of Mexico During 13 Months (October 1973–October 1974)

	Offshore station														Estuarine station											
	Mts.	O	N	D	J	F	M	A	M	J	J	A	S	O	Mts.	O	N	D	J	F	M	A	M	J	J	A	S	O
Phylum Euglenophyta																												
	0														0													
Eutreptia sp.	0														0													t
Phylum Chlorophyta																												
	2	t								t					7			t				t	t	t		t	t	t
Genus unknown	3	b							b	b					5				b					b	b	b	b	
Phylum Pyrrophyta																												
	1								T						0													
Ceratium sp.	2					b						b			0													
Dinophysis sp.	1									T					0													
	0														0													
Gyrodinium sp.	1												t		7		t			t	t			t	t	t	t	
	3						b					b	b		6		b			b	b			b		b	b	
Peridinium spp.	2			t				t							0													
	1										b				0													
Prorocentrum sp.	5					t	T		t	t		t			5					T	t	t				t	t	
	3					b	B					b			2					b						b		
Genus unknown	0														2	t								t				
	0														0													
Phylum Chrysophyta																												
	3		t	t			t								0													
* Dictyocha sp.	1								b						0													
* Ebria sp.	0														1		t											
	0														0													
* Genus unknown	0														1	T												
	0														0													
Amphipora sp.	0														1									t				
	0														0													
Asterionella sp.	2						t					t			3		t	T		t								
	0														2						t					b		
Biddulphia sp.	3				t				t				t		1													t
	3							b	b				b		3								b			b		b
Chaetoceros spp.	4						t			t	t		t		5					t			t		t		t	t
	5			b					B	b	b		b		8			b	b	b	b		b		b	b	b	
Coscinodiscus spp.	12	t	t		T	T	t	t	t	t	t	t	t	t	9	t	T	t	t	t			t			t	t	t
	11	b	b	b	b	B	b		b	b	b		b	b	11	B	B	b	b	b	b		b	b		b	b	b
Detonula sp.	6			t	t			t	t		t				2								t					t
	1			b											1							b						
Ditylum sp.	3									t	T		t		4		t		t		t						t	
	3				b		b						b		1		b											
Eucampia sp.	1								t						0													
	0														0													
Grammatophora sp.	1									T					1										t			
	1														0													
Guinardia	0														1					t								
	0														1					b								
Gyrosigma	1												t		7		t			t	t			t	t	t	t	
	3						b				b	b			6		b			b	b			b		b	b	
Hemialus	1										t				0													
	0														1									b				

| | | |

and operation of hardware and for his continual field assistance. Dr. O. Jenkins generously provided his time and patience for all stastical computations.

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LITERATURE CITED

DAWSON, C. E. 1955. A study of the oyster biology and hydrology at Crystal River, Florida. *Publs Inst. mar. Sci. Univ. Tex.* **4**:279–302.

GALTSOFF, P. S. 1964. The American oyster. *Fishery Bull. U.S. Fish Wildl. Serv.* Vol. **64**, 480 pp.

GUNTER, G. 1951. The West Indian Tree oyster on the Louisiana Coast and notes on growth of the three Gulf Coast oysters. *Science.* **113**:516–517.

———— and R. A. GEYER. 1955. Studies on fouling organisms of the northwest Gulf of Mexico. *Publs Inst. mar. Sci. Univ. Tex.* **4**:38–67.

HOFSTETTER, R. P., T. L. HEFFERNAN and B. D. KING. 1965. Oyster (*Crassostrea virginica*) mortality studies along the Texas Coast. Proj. No. MOR-7, *Proj. Rep. Texas Parks & Wildl. Dept. Coastal Fish.* **1965**:119–131.

HOPKINS, E. E. 199. Determination of condition of oysters. *Science.* **110**:567–568.

MACKIN, J.G. 1962. Oyster disease caused by *Dermocystidium marinum* and other microorganisms in Louisiana. *Publs Inst. mar. Sci. Univ. Tex.* **7**:132–299.

————, H. M. OWEN and A. COLLIER. 1950. Preliminary note on the occurrence of a new protistan parasite, *Dermocystidium marinum* n. sp. in *Crassostrea virginica. Science.* **111**:328–329.

———— and S. M. RAY. 1966. The taxonomic relationships of *Dermocystidium marinum. J. Invert. Pathol.* 8:544–555.

MENZEL, R. W., N. C. HULINGS, and R. R. HATHAWAY. 1958. Causes of depletion of oysters in St. Vincent Bar, Apalachicola Bay, Florida. *Proc. Natl. Shellfish Assoc.* **48**:66–71.

PRICE, W. A. 1954. Oyster reefs of the Gulf of Mexico. *In*: Galtsoff, P. A. (ed.) Gulf of Mexico, Its Origin, Waters and Marine Life, *Fishery Bull. U.S. Fish Wildl. Serv.* **89**:491.

RAY, S. M. 1952. A culture technique for the diagnosis of infections with *Dermocystidium marinum* in oysters. *Science.* **116**:360–361.

————. 1954. Biological studies of *Dermocystidium marinum*, a fungus parasite of oysters. Rice Inst. Pamphlet, Spec. Issue Nov. 1954, 113 p.

————. 1966. A review of the culture method for detecting *Dermocystidium marinum*, with suggested modifications and precautions. *Proc. Natl. Shellfish. Assoc.* **54**:55–69.

———— and A. C. CHANDLER. 1955. *Dermocystidium marinum*, a parasite of oysters. *Exptl. Parasitol.* **4**:172–200.

ST. AMANT, L. S. 1938. Studies on the biology of the Louisiana oyster drill *Thais floridana haysae* Clench. Master's Thesis, La. St. Univ. and A&M College, 108 p.

STRICKLAND, J. D. H. and T. R. PARSONS. 1968. A practical handbook of seawater analysis. *Bull. Fish. Res. Bd. Canada.* **167**, 311 p.

WELLS, H. W. and I. E. GRAY. 1960. Some oceanic subtidal oyster populations. *Nautilus.* **73**:139–147.

STUDIES ON THE EYES OF *HYDROLAGUS* (PISCES: CHIMAERIDAE)

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The Marine Biological Association of the United Kingdom, Plymouth, England, and The University of Texas at Austin

University of Texas Marine Science Institute Contribution No. 253

ABSTRACT

The chimaerids *Hydrolagus affinis* and *H. colliei* have a tapetum lucidum located in the chorioid. It consists of a layer of reflecting cells whose orientations change from parallel to the surface of the retina in the central fundus to very oblique at the periphery of the eyes. The whole fundus is bright in *H. affinis*; in *H. colliei* black pigment extends inwards over the tapetum in extracentral regions, to an increasingly greater extent towards the periphery, and the ventral fundus is black. The reflecting cells contain hexagonal crystals of guanine, their surfaces exhibit a medley of colours, and the overall color of the tapetum is light green. *H. affinis* has a golden rhodopsin, λ_{max} 484 nm, similar to that reported for *H. colliei*. The former is a deep-sea species, the latter coastal, and several features of their eyes are compared with reference to photic conditions in the environment.

INTRODUCTION

Studies of the chimaerid eye have dealt with the tapetum lucidum, retinal absorption, and spectral absorption of the visual pigments (Franz 1905, Denton and Nicol 1964, Nicol and Van Baalen 1968, Crescitelli 1969, McFarland 1970). In this paper the tapeta of *Hydrolagus affinis* and *H. colliei* are described, spectrum absorption characteristics of the visual pigment of *H. affinis* presented, and the eyes of the two species compared.

MATERIALS AND METHODS

Ratfish *Hydrolagus colliei* (Lay and Bennett) were trawled in waters of the San Juan Archipelago. Fresh preparations of eyes were immersed in selachian Ringer and examined microscopically, either by oblique or vertical illumination. A small gimbals table was sometimes used to orient preparations. The term "stripped tapetum" refers to pieces of eyes from which the retina had been removed, leaving the pigment epithelium and chorioid attached to the sclera. Eyes for histology were preserved in Bouin, Helly and Witmaack fixatives, sectioned in wax and celloidin, and stained with haematoxylin and eosin.

Hydrolagus affinis (Cappelo) were captured on long lines at depths of 1920–2323 m in the Bay of Biscay (Forster 1968). Retinae were removed in dim red light and were stored in liquid nitrogen for later examination. They were washed 4x with dogfish Ringer, hardened in 4% iron alum, washed 2x with water, and extracted with 1% digitonin (Dartnall 1957). A refrigerated centrifuge was used in the washing procedure. The extract was made alkaline with sodium

borate (pH 8.6), and spectrum absorbance was measured in a Beckman recording spectrophotometer (Model DK2) before and after bleaching (in white fluorescent light) for 10 min.

OBSERVATIONS

The Eye of **Hydrolagus colliei**

The pupillary aperture is large, the pupil is immobile and shines conspicuously at certain angles of view, that is, when illuminated and viewed in nearly the same direction, either laterally or obliquely from below. A ratfish photographed underwater by SCUBA-divers presents in lateral view a moderately shiny pupil about as bright as the shiny skin adjacent to it (Figure 1).

The tapetum lucidum over much of the eye is light metallic blue in general view. The ventral field is black. A narrow band having a faint purple cast extends almost horizontally across the equator of the eye. The surface of the tapetum has an appearance like that of selachians, and the reflecting cells contain elongate hexagonal crystals which are mostly yellow or blue, blue-green or, less often, rose-colored. Viewed microscopically, nearly normal to the surface, the tapetum is a light green which changes to blue to white at greater angles of incidence.

A piece of stripped tapetum was mounted on a gimbals table and examined microscopically by vertical illumination (Leitz No. 3 objective). Maximal reflection occurred within ± 10° of the vertical.

A layer of black pigment cells or melanophores associated with the tapetum lucidum is organized much like that of selachians (Nicol 1964), that is, the cells form a single layer on the outer surface of the tapetum and send pigmented

FIG. 1. Ratfish photographed underwater; note faint eyeshine.

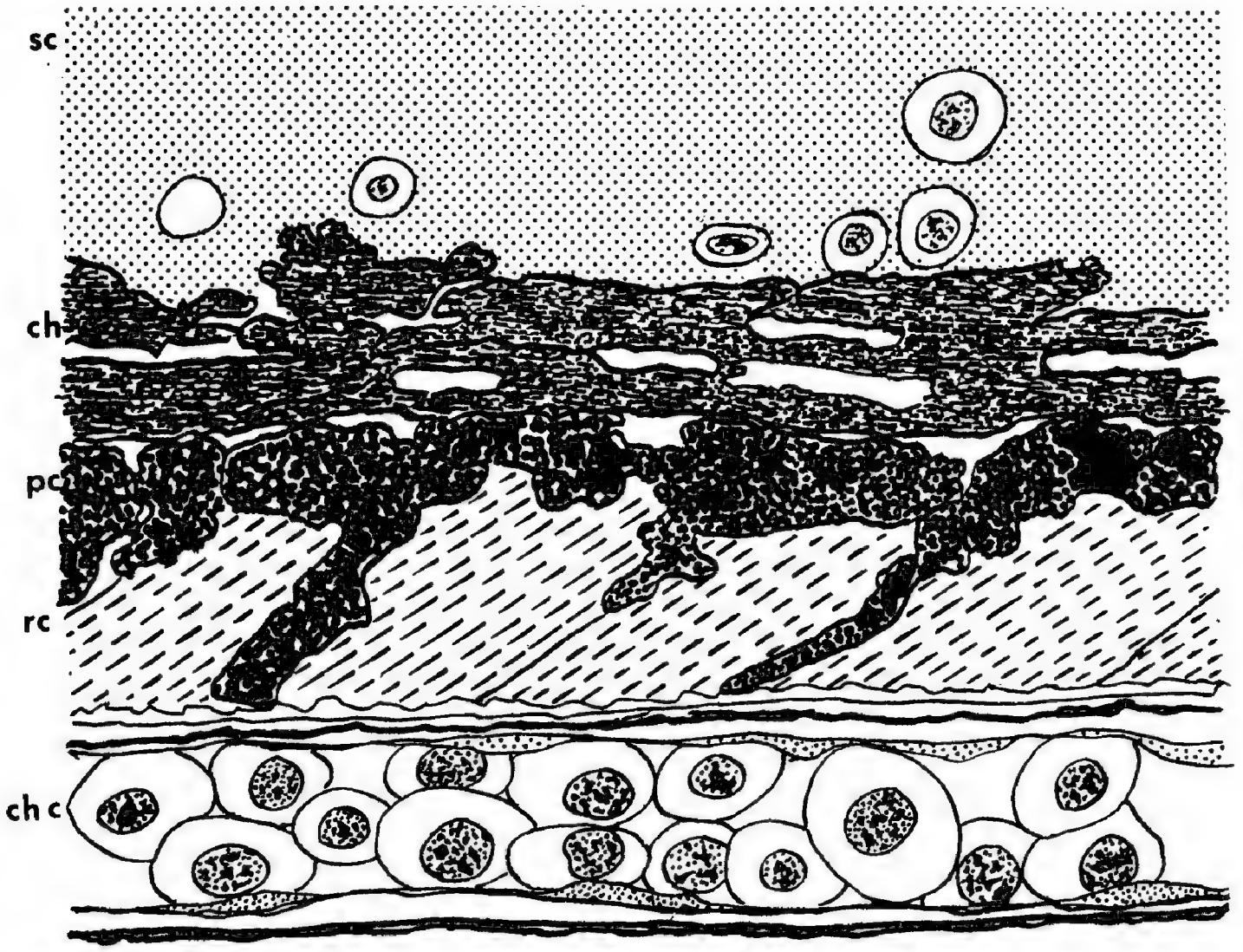

FIG. 2. Appearance of the outer chorioid of the ratfish. Drawing made from a photomicrograph. X approx. 1000. Symbols: Ch, chorioid tissue; ch. c, choriocapillaris; pc, pigment cell; rc, reflecting cell; sc, sclera.

processes inwards between the tapetal cells (Figure 2). As they extend inwards and centripetally over the surfaces of the reflecting cells, they partly or largely obscure them. In general, the pigment is greatly expanded in the ventral field, gradually retracted to a minimum towards the central fundus, where no pigment is visible on the inner surface of the reflecting cells, and progressively expanded again dorsally. Similarly, in a horizontal plane through the center of the eye, the pigment is least expanded in the center and is increasingly expanded towards the periphery. At the periphery, although a good deal of the reflecting surface is covered, it is not nearly as dark as the black ventral field (Plate I, Figures 3 to 10; Figure 11). The pigment is static and the tapetum is not occlusible.

Orientation of Reflecting Platelets in the Tapetum Lucidum

The tapetum is a specular reflector (Denton and Nicol 1964) and is made up of cells containing stacks of flat crystals (*v. infra*). A pile of crystals presenting a localized reflecting surface has been termed a reflecting platelet. The orientation of the reflecting platelets relative to the surface of the tissue in *Hydrolagus colliei* was determined in fresh material. A vertical strip that included the optic nerve

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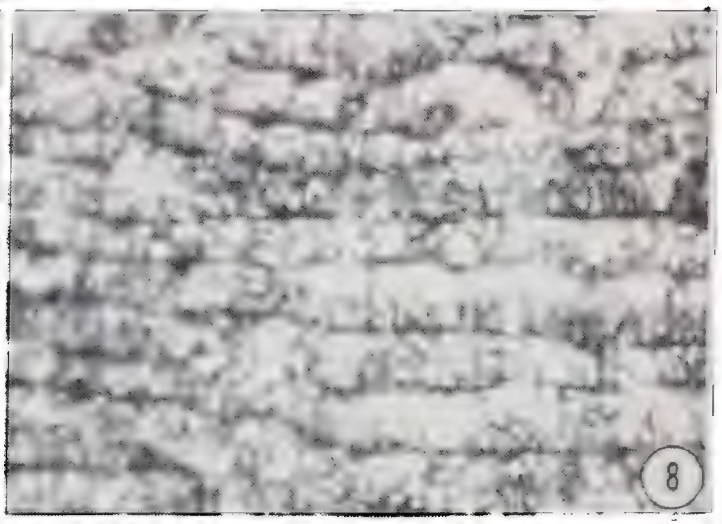
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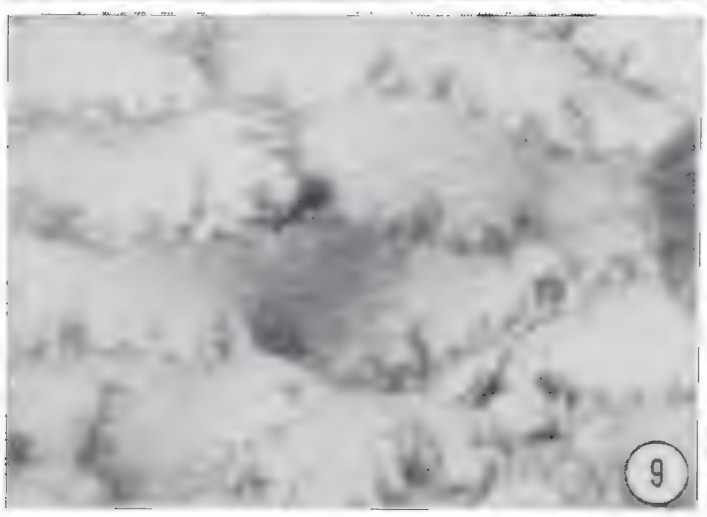
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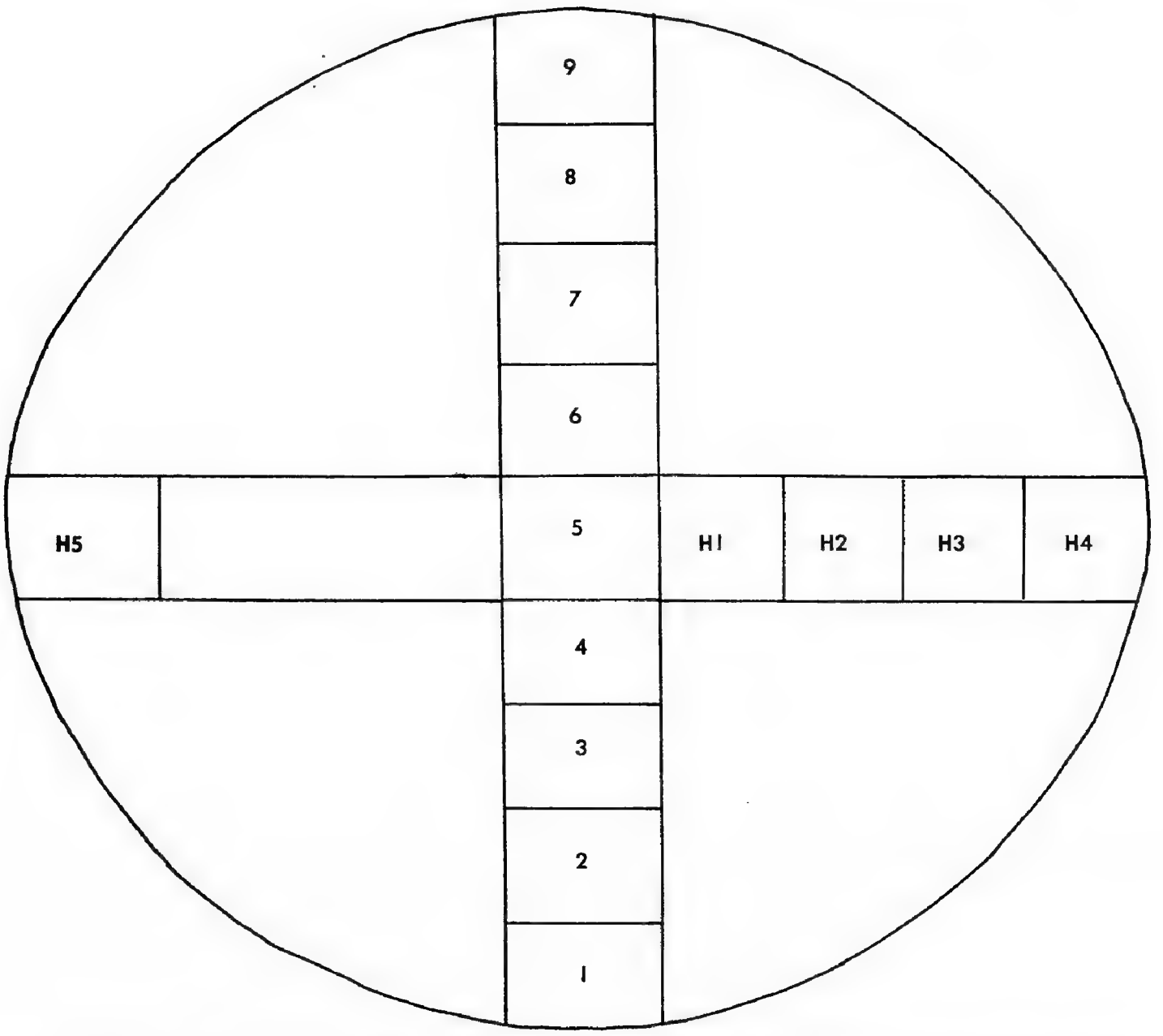

FIG. 11. Regions of ratfish tapeta examined and photographed (see p. 80 of text); selected photographs shown in Plate 1, Figures 3–10.

was cut from the wall of the eyeball. The tapetum lucidum was divided into eight equal pieces which were examined on a small gimbals table, and the angles of tilt were determined. The results are depicted in Figure 12. It is seen that, measured in a vertical or dorso-ventral direction, the platelets are parallel or nearly parallel to the surface of the tissue in the central fundus, and become increasingly tilted away from this surface towards the margin of the eye. In the

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FIGS. 3–10. Surface views of stripped tapeta of the ratfish, taken from areas indicated in Figure 11. Figures 3 to 8, vertical band; 9 and 10, horizontal band. X 146.

Fig.	Area	Fig.	Area
3	5	7	6/7
4	4	8	8
5	3	9	H 2
6	2	10	H 5

other plane (i.e., in a horizontal or rostro-caudal direction) the surfaces of the platelets are in most directions nearly parallel to the surface of the tissue.

The orientation of reflecting cells in a vertical histologic section is shown in Figure 13. Because the crystals lie mostly parallel to the surfaces of the cells, the

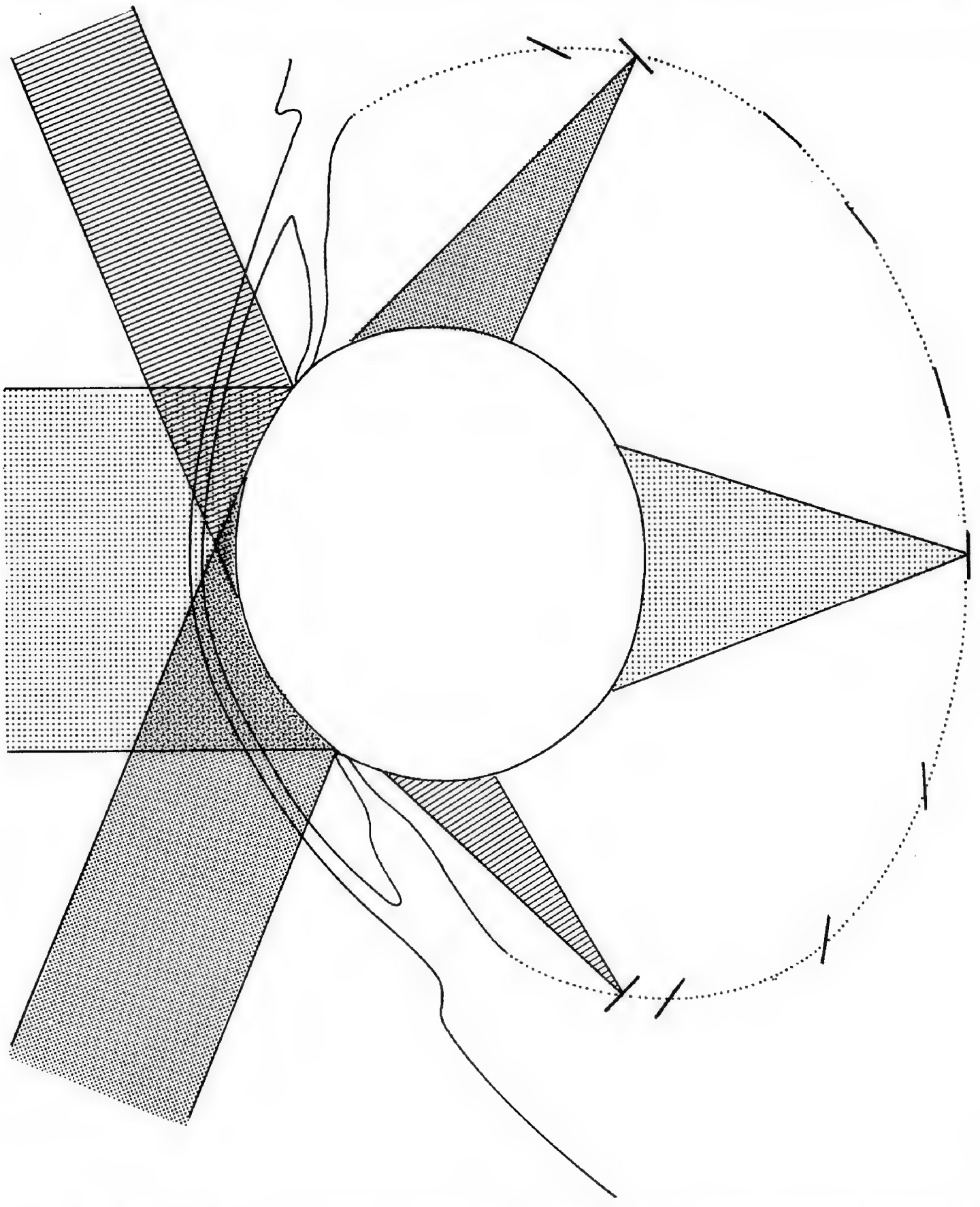

FIG. 12. Vertical section through the eyes of the ratfish to show the approximate orientation of reflecting platelets, as determined by an optical method (see text for details). Also shown is how parallel beams from three directions impinge upon the tapetal plates.

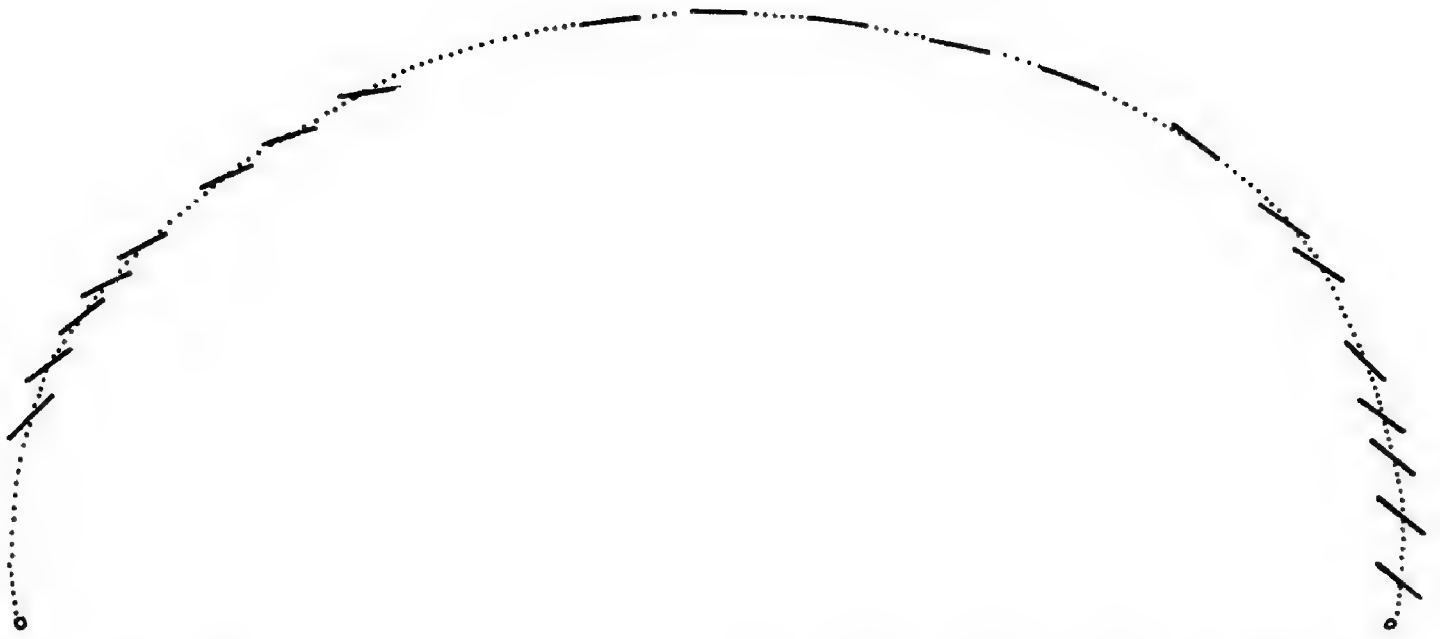

FIG. 13. Orientation of reflecting platelets in a vertical section through the eye. From measurements made on celloidin and paraffin sections.

orientation of the cell is the orientation of the reflecting surface or platelet. Comparison of Figures 12 and 13 shows that there is good agreement between the results derived from the experimental and histological procedures.

Crystals

The shiny appearance of the tapetum is produced by small, flat crystals of guanine stacked in tiers within the reflecting cells (Nicol and Van Baalen 1968). Tapetal tissue was gently teased and the crystals were released into distilled water. They were elongate hexagons, similar in size and shape to those of selachians; many showed similar lacunae; and they exhibited the same interference colours (Denton and Nicol 1964, Best and Nicol 1967).

Histology

The eye is nearly globular, somewhat compressed in the upper half; it is thin-walled and easily deformed. The cornea is thin and the iridial curtains leave a large pupillary aperture. Eyelids extend well over the upper and lower surfaces of the eyeball and front of the iris.

The outer region of the chorioid is densely pigmented and packed with melanocytes; the inner contains the tapetum lucidum. Reflecting cells of the tapetum form a layer several cells deep immediately adjacent to the choriocapillaris (Figure 2). They are elongated flattened cells whose plane surfaces face the retina. In the center of the eye the reflecting cells lie more or less parallel to the surface of the retina and, progressing towards the periphery, they become increasingly oblique to the surface (*v. supra*) (Figure 13).

The tapetum is backed by a row of melanophores (Figure 2), pigmented processes of which extend some way internally over the tapetal plates. In the

central fundus the pigment does not reach the inner surface of the chorioid. In the ventral tapetum a large part of the surface is covered by the pigmented processes of the tapetal pigment cells, which extend inwards beneath the choriocapillaris. In the dorsal tapetum the pigmented processes also extend inwards, but they are not as dense or continuous as they are in the ventral pimented field.

The pigment epithelium (in section) is made up of cuboidal cells lacking pigment granules. The visual elements are all rods, slender and closely packed. They lie normal to the surface of the retina and the outer segments abut against the cells of the pigment epithelium. Outer and inner segments are slender, about 3 μm wide. In the central retina outer segments are 22 μm long, 19 μm in the ventral retina, and 13–15 μm in the dorsal retina.

Observations of **Hydrolagus affinis**

The retina of *H. affinis* was yellow and an extract of visual pigment absorbed maximally at 484 nm. Absorption maxima in the u.v. occurred at about 340 and 277 nm (cf. λ 345 and 275 nm for purified bovine rhodopsin (Collins *et al.* 1952)). Maximal absorbance of the bleached pigment and the isosbestic point occurred at 369 nm. The wavelength maximum of the difference spectrum, based on nomogram analysis (Dartnall and Lythgoe 1965) was 484 nm; the ratio of D_{min}/D_{max} was 0.25.

Rod outer segments were measured in Ringer: they were 43.2 to 48.8 μm long (mean 46.6 μm). In preserved material the length was 46 μm (Denton and Nicol 1964).

DISCUSSION

The two species of chimaerids examined, viz. *Hydrolagus colliei* and *H. affinis*, have pure rod retinae. Both have chorioidal tapeta lucida which are essentially similar, consisting of a layer, several cells deep, of reflecting cells packed with flat crystals of guanine. The reflecting cells are regularly oriented and the iridial curtains act as stops, restricting light destined for the periphery of the eye to the outer regions of the lens. As a consequence, light falls upon the reflecting cells approximately normal to their surfaces, as depicted in Figure 12. A similar situation exists in *H. affinis* (Denton and Nicol 1964).

The refractive index of the rods is higher than that of the intercellular fluid and vitreous, and light is channelled through the outer segments, which lie close to the tapetal surface. Consequently, there is little spread of light, reflection is specular, and the arrangement is one that does much to reduce the spread of light within the eye. It is not known whether the rods, towards the periphery of the eye, are directed towards the center of the lens, or are oriented vertically to the retinal surface. In the latter event light, exceeding the critical angle of the rod outer segments, must pass obliquely through several rod outer segments. The light is reflected inwards over the same path to the lens, or to the inner surface of the iris to be absorbed (Denton and Nicol 1964, Nicol 1977).

In the ratfish *Hydrolagus colliei* the black pigment associated with the tapetum lucidum is expanded to a various extent in different regions of the retina. The ventral field is black, the pigmented processes decrease and disappear towards the central fundus and, in the dorsal and lateral regions of the tapetum, some pigmented processes again extend over the tapetal plates.

A very small dark ventral field is present in the tapetum of *Chimaera monstrosa* (Franz 1905).

The ratfish shows eyeshine, and its skin also is very lustrous, containing a layer of oriented reflecting cells much like those of the tapetum lucidum (Arnott and Nicol 1970). Therefore, light emerging from the pupil is seen by an observer and compared against both background illumination and light reflected from the exterior of the fish. It will be recalled that there is differential expansion of pigment over the tapetum from the central fundus (negligible) to the periphery, and that submarine illumination decreases at increasing angles of tilt (Jerlov 1968). Because of these factors, the luster of the body and eyeshine are about as bright as the background. Submarine photographs of ratfish made by SCUBA-divers show that the brightness of the pupil in lateral view is about the same as reflection from the side of the head (Figure 1). The greatest mismatch concerns the dorsal fundus, as might be expected because the animal can do nothing to secure more light from the region below it. Because the ratfish is nocturnal in habits, remaining near the bottom during the day, the dorsal field of the eye is not one that is much exposed to view when the ambient light is bright. Probably of more importance (to the fish) is the brightness of the pupil compared with that of the immediately adjacent surround of the head (Cott 1940). Mottling of the skin in that region and the way in which the platelets in the skin below the eye face downwards, must make the pupil a less salient feature.

The eyes of two species of *Hydrolagus* have now been examined, viz. *H. affinis* (Nicol 1964, Denton and Nicol 1964) and *H. colliei*. The former is a deep-sea species, occurring in moderately deep to deep water, from 290 to 2350 m, and the later is found on the shelf, from the shallows to 366 m (Bigelow and Schroeder 1953; Clemens and Wilby 1961; Forster 1964, 1968, 1973; Arnott and Nicol 1970). The appearance of the tapetum in the two species is dissimilar: the whole surface of the tapetum of *H. affinis* is bright whereas that of *H. colliei* is regionally pigmented. These differences may be related to the different light regimes encountered by these animals. In the deep waters where *H. affinis* is found, below 500 m or so, the illumination is largely or entirely luminescence, liable to come from any direction, and devices to reduce eyeshine in particular directions are, perhaps, of no significance. Moreover, because of the high optical density of the visual pigment, it is unlikely that more than one-tenth of the light that enters the pupil is reemitted.

Neither species has a mechanism for regulating the amount of light entering the eye and affecting the visual cells. The pupils are immobile, and no migration of pigment takes place across the tapetal surface (Nicol 1964).

The rod outer segments of *H. affinis* are about twice as long as those of *H. col-*

liei; the maximal retinal density measured in the former is about 0.38, and it probably is about 0.20 in *H. colliei* (estimated from the curve in Figure 19 of Denton and Nicol 1964), i.e., about the same as in a coastal selachian. It is very likely that the density of visual pigment in *H. affinis* is about twice that in *H. colliei*.

The visual pigment of *Hydrolagus colliei* is a rhodopsin absorbing maximally at 484 nm (VP 484_1) (Beatty 1969, Crescitelli 1969). The visual pigment of *H. affinis* also shows maximal absorption at 484 nm. This value is in agreement with the spectrum absorption curve for retinal density of *H. affinis*, namely λ_{max} 484 nm, measured *in vitro* (recalculated from the curve in Denton and Nicol 1964). The absorption maximum of the spectrum of the visual pigment, the higher optical density of the retina, and the uniformly bright tapetum of *H. affinis* are positively related to the spectrum composition and weak intensity of deep-water illumination. In the total absence of downwelling illumination from the surface at the great depths inhabited by *H. affinis*, only light from bioluminescent animals, often blue in colour, is available for vision (Clarke and Denton 1962). The retinae of deep-sea squaloid sharks (*Centroscymnus coeolepis*, *Centrophorus squamosus*, *Deania calcea*), caught in the same region and at the same depths as *Hydrolagus affinis*, have golden retinae, and their visual pigments show maximal absorption in the range 475 to 484 nm (Denton and Shaw 1963).

Hydrolagus colliei has a rhodopsin absorbing maximally at 484 nm. A golden rhodopsin is unusual in a fish from the continental shelf; it may be a characteristic retained unaltered during invasion of a coastal environment. The visual pigment of the elephant fish *Callorhinchus callorynchus* (another chimaeroid fish) is a rhodopsin with absorption maximum at 499 nm. This is a shallow-water species taken commonly at depths of 10m, although extending down to 180 m (McFarland, 1970). Coastal waters may be expected to have maximal light transmission in the green, at 500 nm and higher.

ACKNOWLEDGMENTS

Some part of this research was carried out during 1967 at the Friday Harbor Laboratories of the University of Washington and the Director and staff are thanked for hospitality and assistance. Specimens of *Hydrolagus affinis* were collected on a cruise of R/V *Sarsia* of the Marine Biological Association of the U.K. in 1966. The investigation was supported by grants from the National Institutes of Health, NB 07867–01, NB 08128–01 and EY 00495–01.

LITERATURE CITED

ARNOTT, H. J. and J. A. C. NICOL. 1970. Reflection of ratfish skin. *Can. J Zool.* **48**: 137–151.

BEATTY, D. D. 1969. Visual pigments of three species of cartilaginous fishes. *Nature, Lond.* **222**:285.

BEST, A. C. G. and J. A. C. NICOL. 1967. Reflecting cells of elasmobranch tapetum lucidum. *Contr. mar. Sci.* **12**:172–201.

BIGELOW, H. B. and W. C. SCHROEDER. 1953. *Fishes of the Western North Atlantic.* Mem. No. 1, Pt. 2, Sears Foundation for Marine Research, 588 pp.

CLARKE, G. L. and E. J. DENTON. 1962. Light and animal life. *In* M .N. Hill (ed.), *The Sea*, vol. 1, pp. 456–468. Interscience, New York.

CLEMENS, W. A. and G. V. WILBY. 1961. Fishes of the Pacific Coast of Canada. *Bull. Fish. Res. Bd. Can.* No. **67**, 368 pp.

COLLINS, F. D., R. M. LOWE and R. A. MORTON. 1952. Studies in rhodopsin. 4. Preparation of rhodopsin. *Biochem. J.* **51**:292–298.

COTT, H. B. 1940. *Adaptive Coloration in Animals*. Methuen, London, 508 pp.

CRESCITELLI, F. 1969. The visual pigment of a chimaeroid fish. *Vision Res.* **9**:1407–1414.

DARTNALL, H. J. A. 1957. *The Visual Pigments*. Methuen, London, 216 pp.

———— and J. N. Lythgoe. 1965. The spectral clustering of visual pigments. *Vision Res.* **5**:81–100.

DENTON, E. J. and J. A. C. NICOL. 1964. The chorioidal tapeta of some cartilaginous fishes (Chondrichthyes). *J. mar. biol. Ass. U.K.* **44**:219–258.

———— and T. J. SHAW. 1963. The visual pigments of some deep-sea elasmobranchs. *J. mar. biol. Ass. U.K.* **43**:65–70.

FORSTER, G. R. 1964. Long-line fishing on the continental slope. *J. mar. biol. Ass. U.K.* **44**:277–284.

————. 1968. Line-fishing on the continental slope, II. *J. mar. biol. Ass. U.K.* **48**:479–483.

————. 1973. Line fishing on the continental slope. The selective effect of different hook patterns. *J. mar. biol. Ass. U.K.* **53**:749–751.

FRANZ, V. 1905. Zur Anatomie, Histologie und funktionellen Gestaltung des Selachierauges. *Jena. Z Naturw.* **40**:697–840.

JERLOV, N. G. 1968. *Optical Oceanography*. Elsevier Publ. Co., Amsterdam, London, New York, 194 pp.

McFARLAND, W. N. 1970. Visual pigment of *Callorhinchus callorynchus*, a southern hemisphere chimaeroid fish. *Vision Res.* **10**:939–942.

NICOL. J. A. C. 1964. Reflectivity of the chorioidal tapeta of selachians. *J. Fish. Res. Bd. Can.* **21**:1089–1100.

————. 1977. Tapeta lucida of vertebrates. *In* J. N. Enoch (ed.), *Topics in Modern Physics. The Optics of Vertebrate Retinal Receptors*. Springer-Verlag, Berlin, Heidelberg, New York. In press.

———— and C. VAN BAALEN. 1968. Studies on the reflecting layers of fishes. *Contr. mar. Sci.* **13**:65–88.

STUDIES ON THE EYE OF THE STINGAREE *DASYATIS SABINA*, WITH NOTES ON OTHER SELACHIANS. I. EYE DIMENSIONS, CORNEA, PUPIL AND LENS

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University of Texas Marine Science Institute Contribution No. 254

ABSTRACT

Measurements of ocular diameters and pupillary apertures of stingarees *Dasyatis sabina* are presented. The position of the optic axis relative to the chief axes of the fish has been determined, pupillary apertures of dark-and-light-adapted eyes have been measured and estimates have been made of the light entering the pupil at various angles of tilt. Changes of pupillary aperture involve both descent of an operculum and iridial constriction; the pupil closes in about 5 min and opens in about 30 min. The corneas of the stingarees examined were cloudy, this condition was a feature of the epithelium. Spectrum transmission of the lens was measured, short wavelengths, below 425 nm, were heavily absorbed. Some consequences of these optic conditions are discussed.

INTRODUCTION

The eye of the stingaree has an unusual combination of features for a selachian, namely a constricting pupil together with an operculum capable of descending over it, abundant cones, and an occlusible tapetum lucidum. In this and succeeding papers the eye of the stingaree and some of its functional characteristics are described. Attention is directed to the tapetum lucidum and its role in the visual process. From time to time the opportunity has arisen of examining the eyes of other elasmobranchs, and some pertinent observations are included when they provide an interesting comparison with the stingaree.

MATERIALS AND METHODS

Stingarees *Dasyatis sabina* (LeSueeur) were collected in shallow water in bays or in the Gulf nearshore in the vicinity of Port Aransas, Texas, by otter trawls.

Measurements of the Pupil

A photographic method was used to measure pupillary aperture and follow iridial movement. Stingarees were anaesthetized (Sandoz MS 222, 50 mg 1^{-1}) and the eyes were photographed at

intervals by electronic flash. Angle of tilt of the camera from the vertical was 75°. A white fluorescent lamp, about 1/11010 daylight intensity (400 lx at 50 cm), was used for light-adapting the animal. When the fish were being dark-adapted, a red filter (cutting off below 600 nm) was placed over the flash unit and very high speed panchromatic film (Kodak Tri-X Pan) was used, which was developed with Acufine film developer. Pupillary areas were measured on tracings made from the film.

Spectrophotometry

Absorption of the cornea and lens was measured in a Beckman DU spectrophotometer. The light beam was reduced to a circle of 1.4 mm diameter. For corneal measurements a piece of opal lucite (opaque below 400 nm) was placed in front of the photomultiplier; for lens measurements a piece of frosted or flashed opal glass was similarly placed. Absorbance of lens homogenate was measured in a Bausch & Lomb spectronic 20, with flashed opal glass behind the cuvettes.

Tissues were mounted or suspended in selachian Ringer solution (Nicholls 1933), modified to contain 0.49g $CaCl_2$ and 0.16 g $MgCl_2$ 1^{-1}, but omitting glucose.

OBSERVATIONS

The eye protruding from the upper surface of the head tilts slightly upwards and medially towards the rostrum; at rest the angle of tilt (optic axis to the vertical) is 54°, and the medial inclination (rostrad) (from the optic axis to the anteroposterior axis) is 72°. When the eye is at rest, the monocular field of view in the vertical plane is about 144° (light-adapted eye, tilt angles of − 12° to 129°) (Fig. 1). In the horizontal plane the monocular field is about 190°, and the binocular field in front of the fish is about 22°.

Dimensions of the eye relative to body weight and size are presented in the graphs of Figs. 2 and 3. Disc length and width were equal within the limits of measurement. A thick knob of cartilage lying on the median wall of the eyeball made for some uncertainty in measuring eye depth. Interrelations of eye dimensions in three planes are shown in Fig. 4.

The eye is flattened in front and the cornea is slightly curved. The fundus forms part of a sphere, and the upper surface is prolonged into a long flat uvea (pars caeca) lacking retina (Figs. 5 and 6).

The upper surface of the iris is provided with an operculum. The lens is flat-

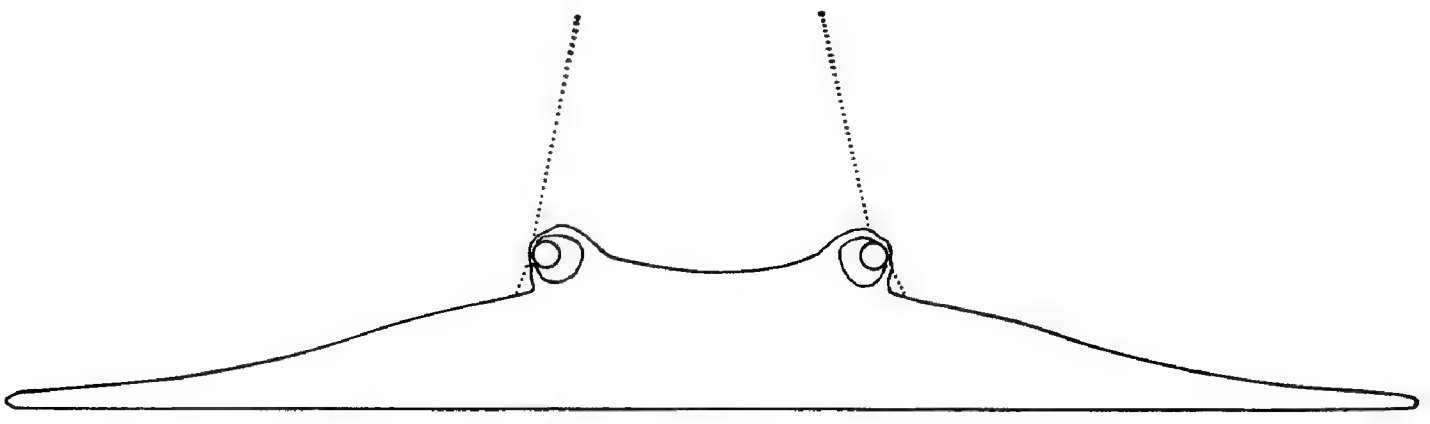


FIG. 1. Transverse vertical section through the body of a stingaree in the plane of the optic axis. Dotted lines, limits of fields of view.

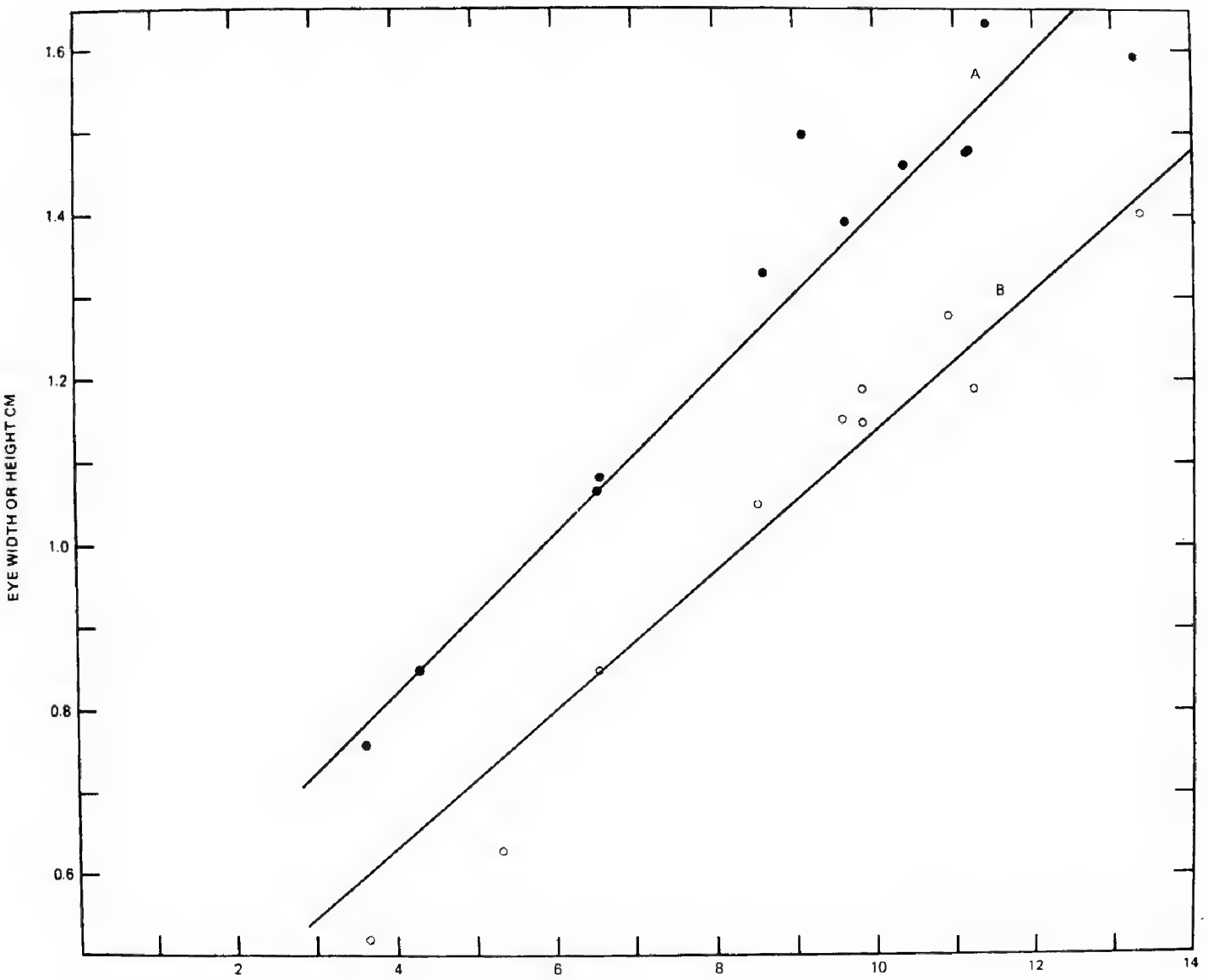


FIG. 2. Stingaree. Eye dimensions (ordinate) versus $\sqrt[3]{}$ body weight. A, width, B, height of eye. In this and in Figs. 2, 3, 4, 8 to 11, regression lines were computed from the data.

tened in the optic axis, and has about the same diameters in dorso-ventral and antero-posterior (i.e. rostro-caudal) directions. Dimensions of the lens, measured in two axes and plotted against eye size, are shown in Figs. 7 to 10.

The Pupil and Iridial Movement

In the rays and stingrays from shallow waters, the dorsal iris bears an operacula flap which descends over the pupil.

In the stingaree the iris constricts and the operculum descends in the light, thereby restricting the pupillary aperture. The process takes place quickly, in about 5 min, and opens more slowly in darkness, in 30–45 min (22–24°C) (Fig. 11.) There is a slight degree of overshoot when the pupil closes, and some variability or oscillation of pupillary aperture after the pupil has opened.

Eyes of light-adapted (L.A.) stingarees were photographed at selected angles of tilt to the vertical to determine relative pupillary apertures presented to radiance arriving at those angles. Results are presented in Fig. 12. Pupillary apert-

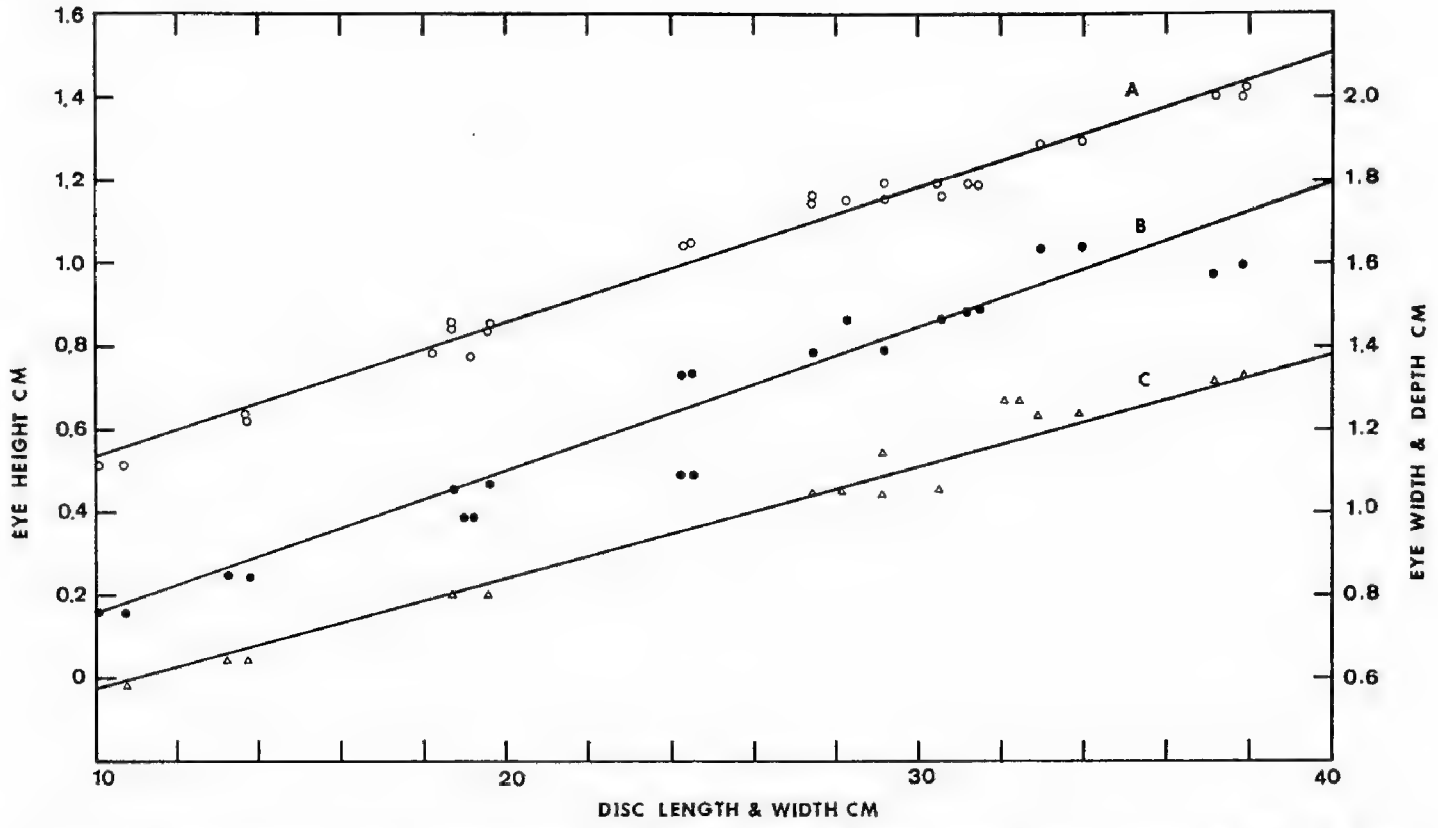


FIG. 3. Stingaree. Eye dimensions (ordinate) versus body size (length and width of disc). A, height, B, width, C, depth of eye.

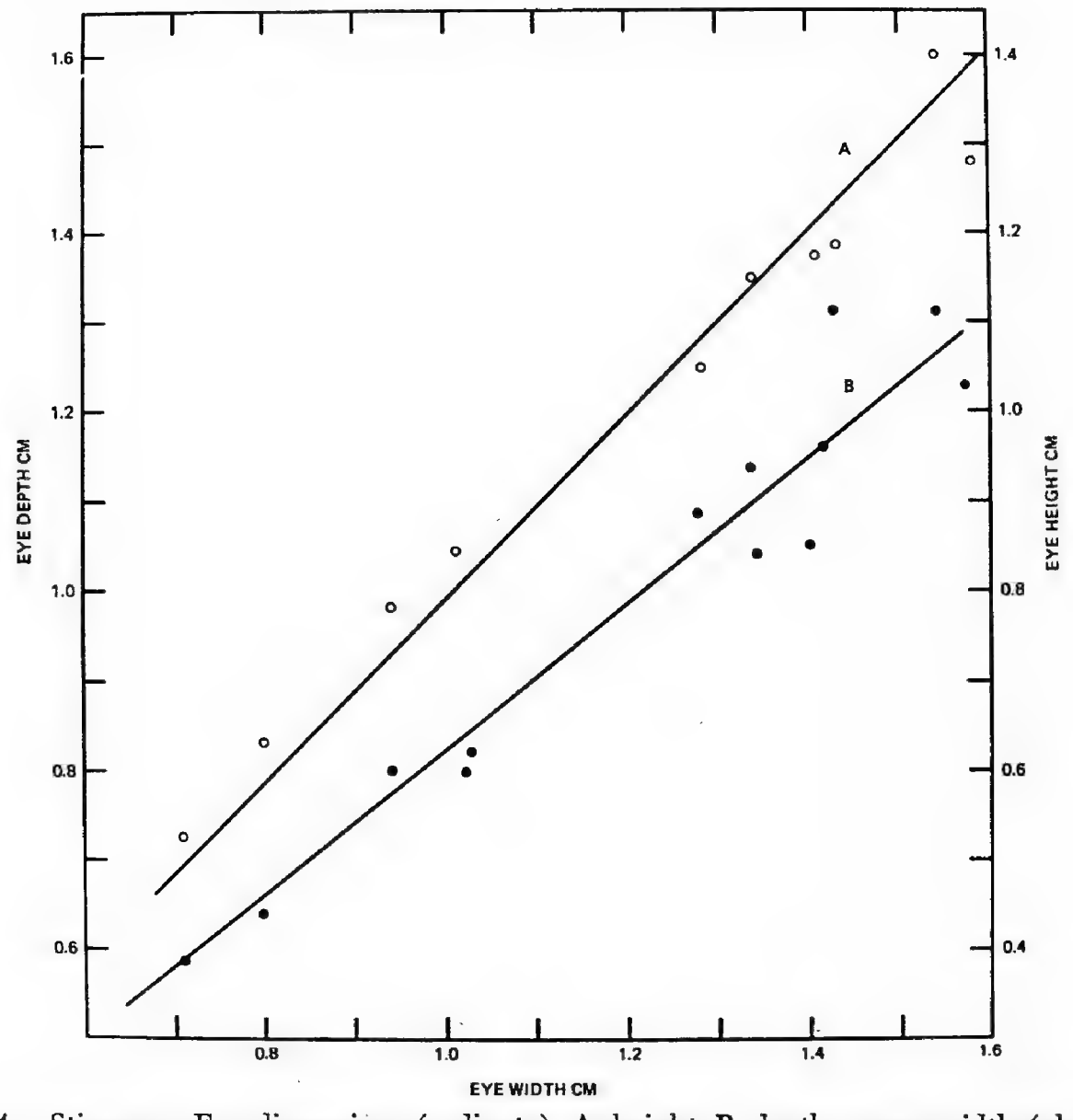


FIG. 4. Stingaree. Eye dimensions (ordinate), A, height, B, depth, versus width (abscissa).

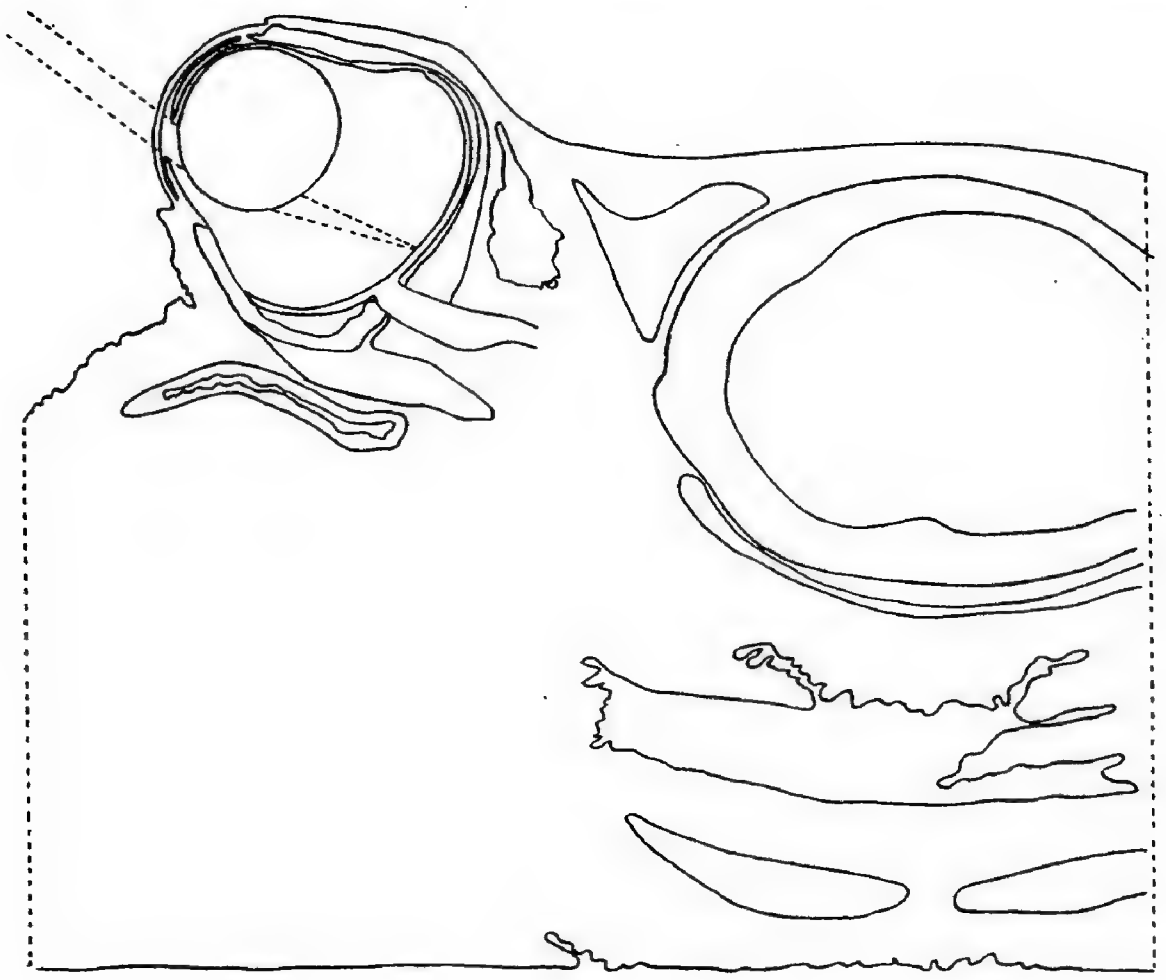


FIG. 5. Transverse vertical section through the head and eye of a stingaree. × 11.7.

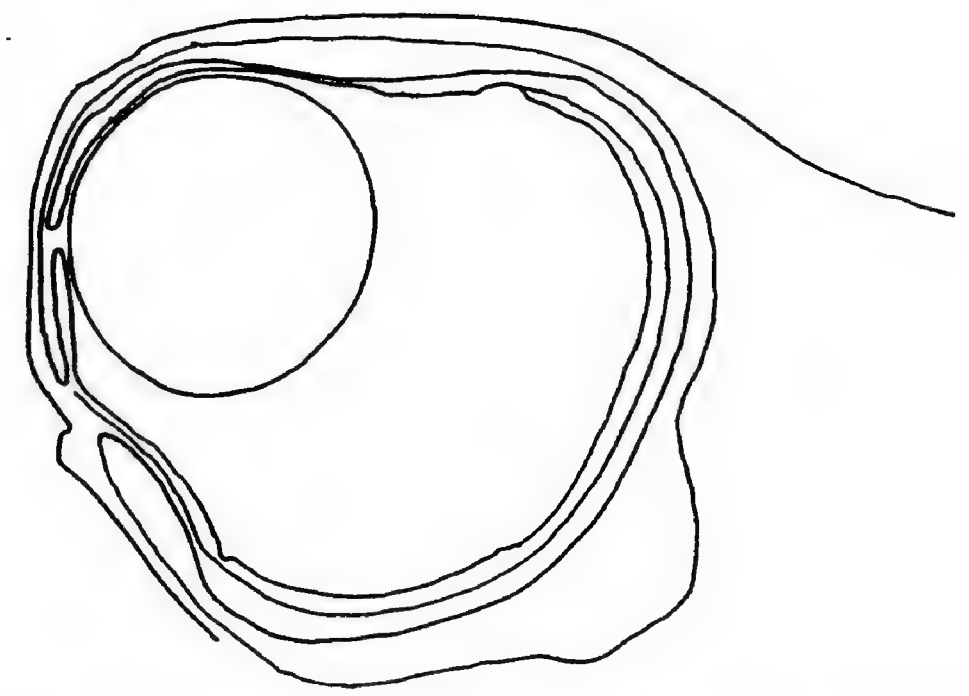


FIG. 6. Vertical section through the eye of a stingaree (operculum descended). × 21.3.

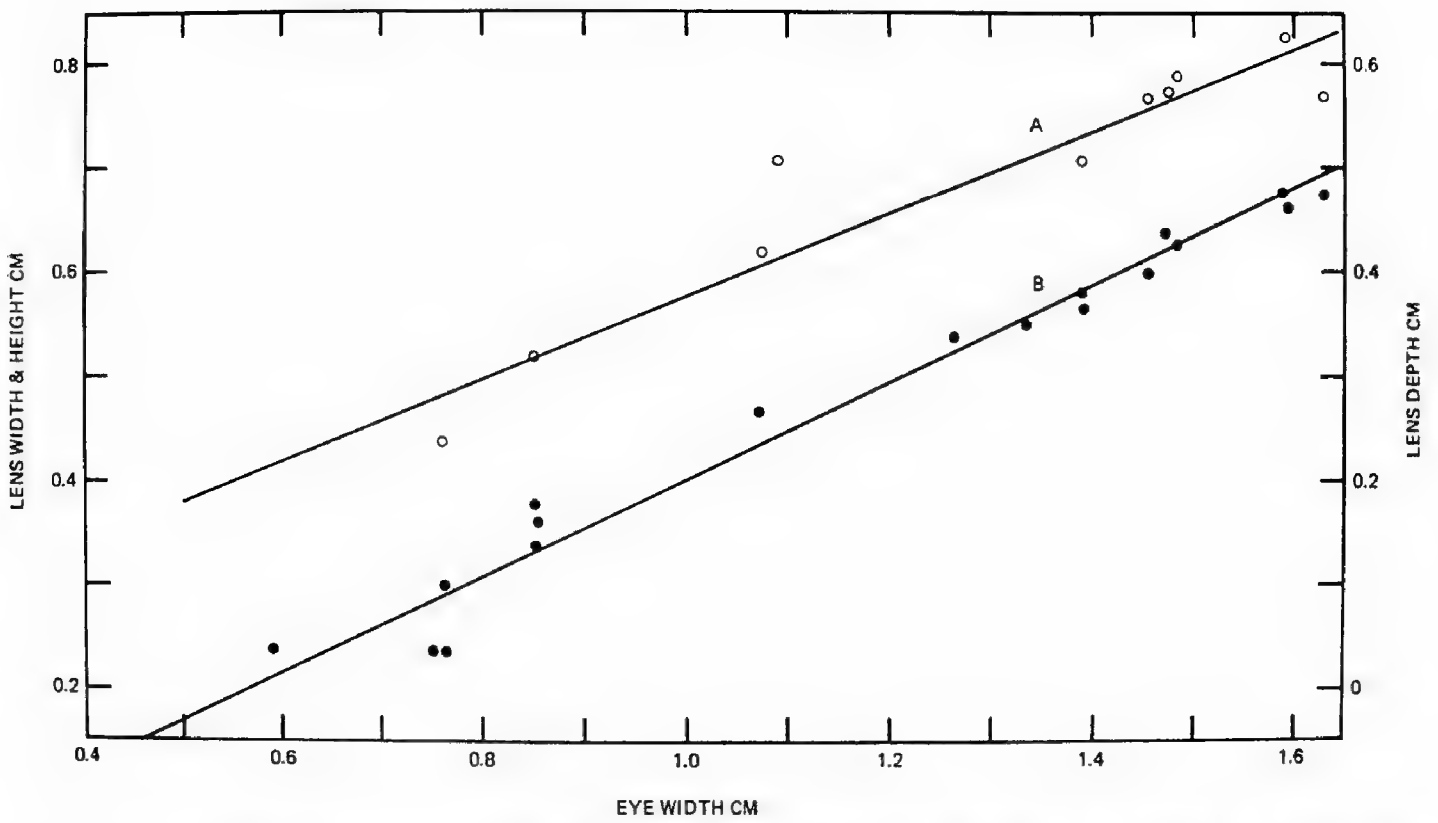


FIG. 7. Stingaree. Lens (ordinate) versus eye dimensions (abscissa). A, depth, B, width and height of lens versus eye width.

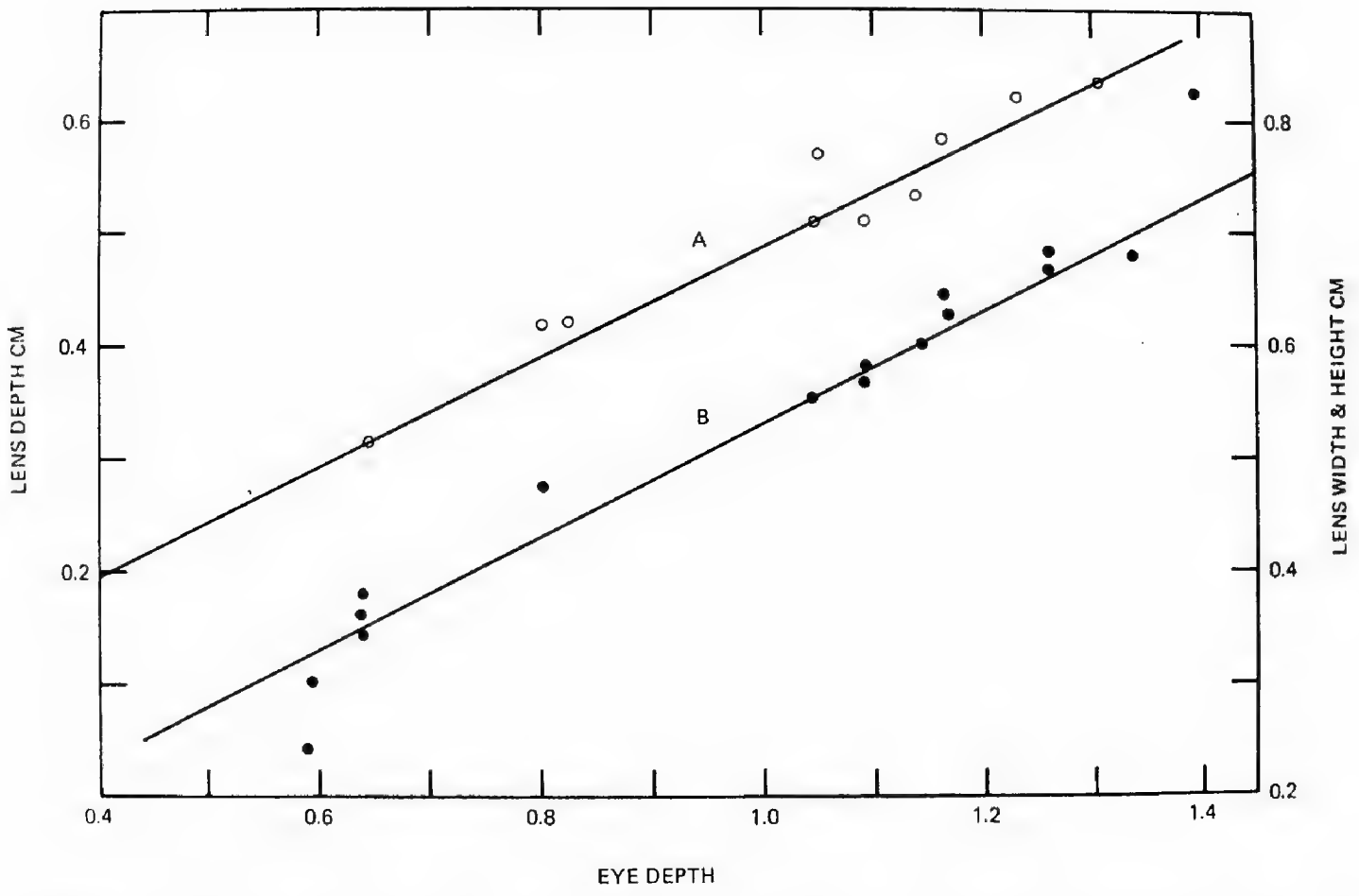


FIG. 8. Stingaree. Lens (ordinate) versus eye dimensions. A, depth of lens, B, width and height of lens versus depth of eye.

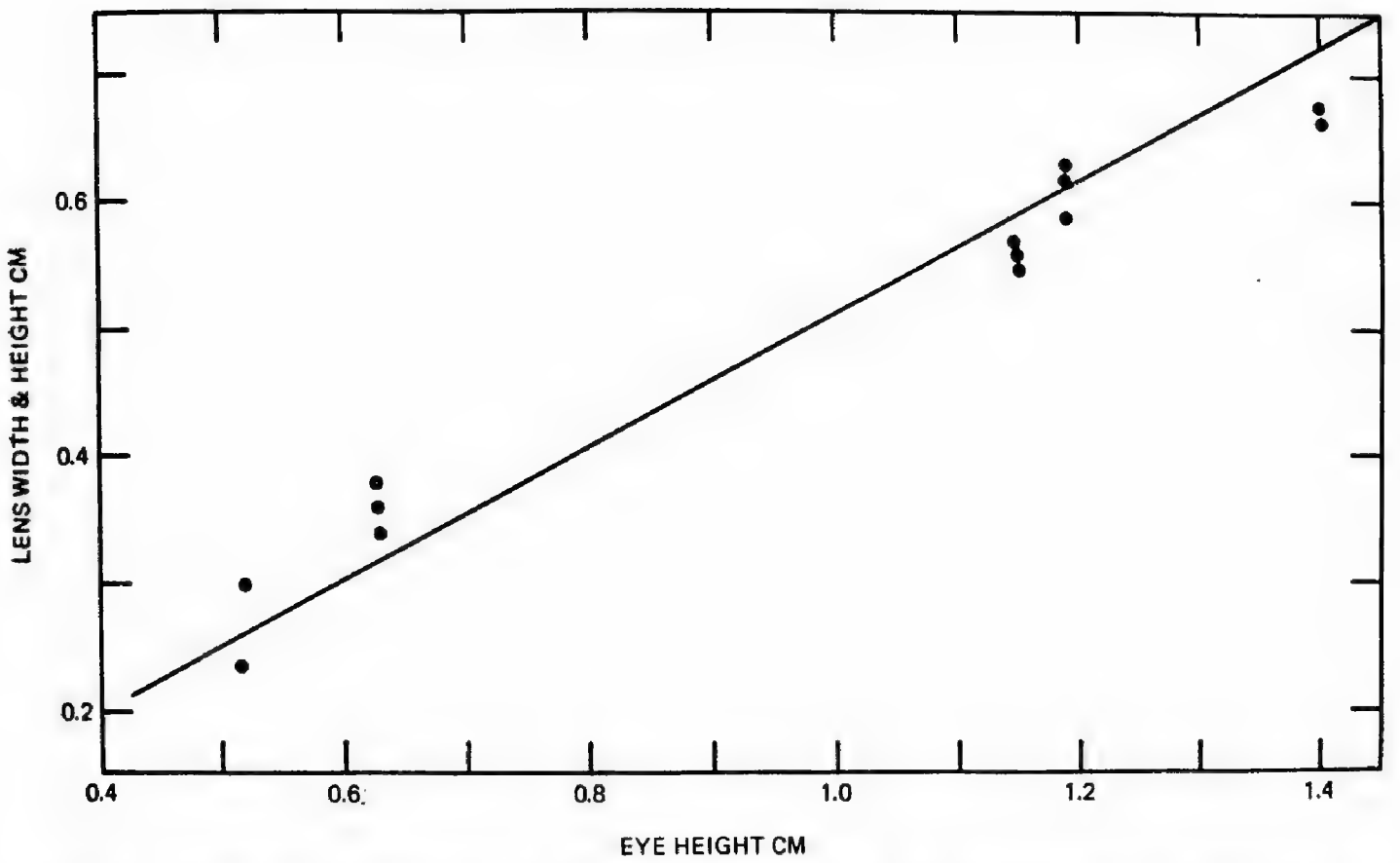


FIG. 9. Stingaree. Dimensions of lens (ordinate), width and height, versus height of eye (abscissa).

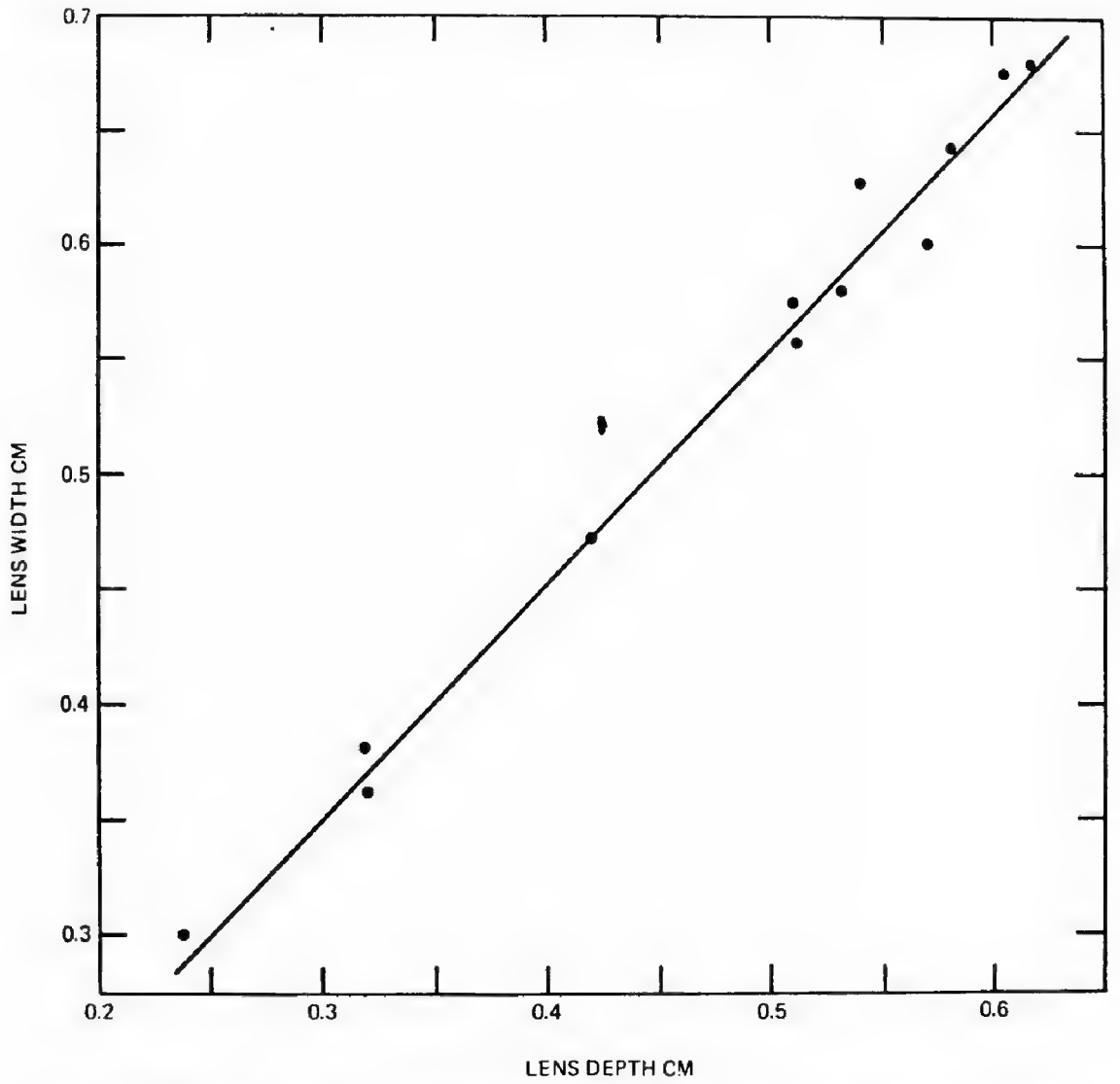


FIG. 10. Stingaree. Dimensions of lens. Width (ordinate) versus depth.

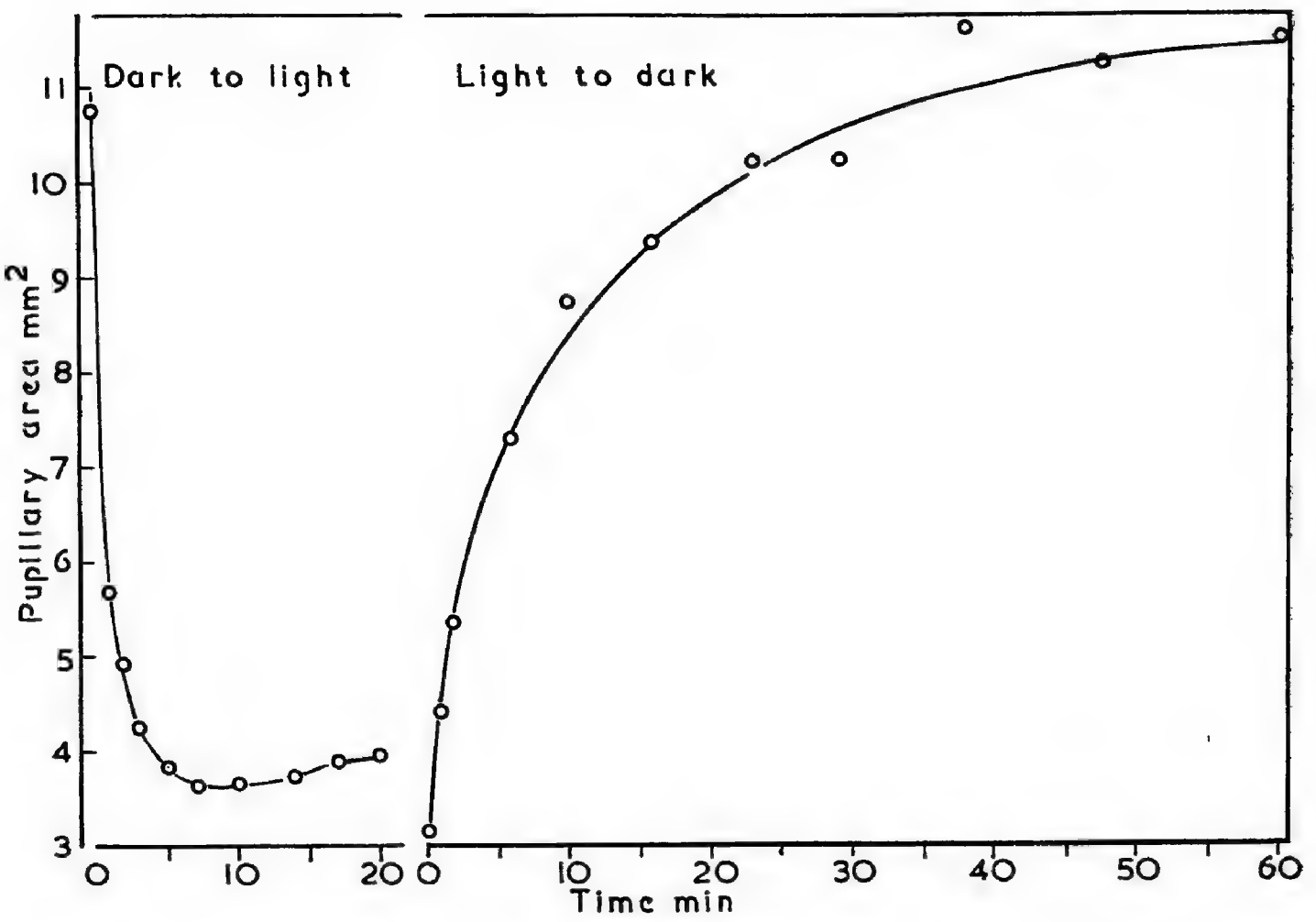


FIG. 11. Change of pupillary aperture of the stingaree. Left, dark-adapted (1 h in darkness), from dark to light. Right, light-adapted fish, light off at 0 min. Temp. 22–24° C.

ture was maximal at 80° (the pupillary plane is approximately normal to light arriving at that angle of tilt), decreasing to 0.88 of the maximum at 54° (in the optic axis), and 0.11 at 0°. Photographs of the L.A. eye at 82 and 2° are reproduced in Figs. 13 and 14.

Pupillary apertures in a stingaree (disc-length 19.1 cm) in light and darkness were measured. The animal, lying horizontally, was photographed at 90° to the vertical; it was kept in darkness for 1h, then exposed to sunlight for ½h (Figs. 15 and 16). The two selected situations are extremes of illumination which the animal encounters. The area of the pupil was 2.3 mm² in light and 8.4 mm² in darkness. Closure of the pupil, therefore, reduces light entering the eyes at angle of tilt of 90° to 0.27 of the maximum.

Other selachians. Pupils of other selachians from epipelagic and coastal waters close quickly (within a few min) and open more slowly (after 30–45 min), e.g. *Scyliorhinus stellaris* and *Negaprion brevirostris* (Young 1933, Kuchnow and Gilbert 1967, Gruber 1967). In deep-sea rays *Raja richardsoni* and *Breviraja* pallida the operculum is rudimentary and the pupil does not close in the light.

Cornea, Lens and Vitreous Humor of the Stingaree

The cornea is colorless and cloudy. The cloudiness, having the appearance of

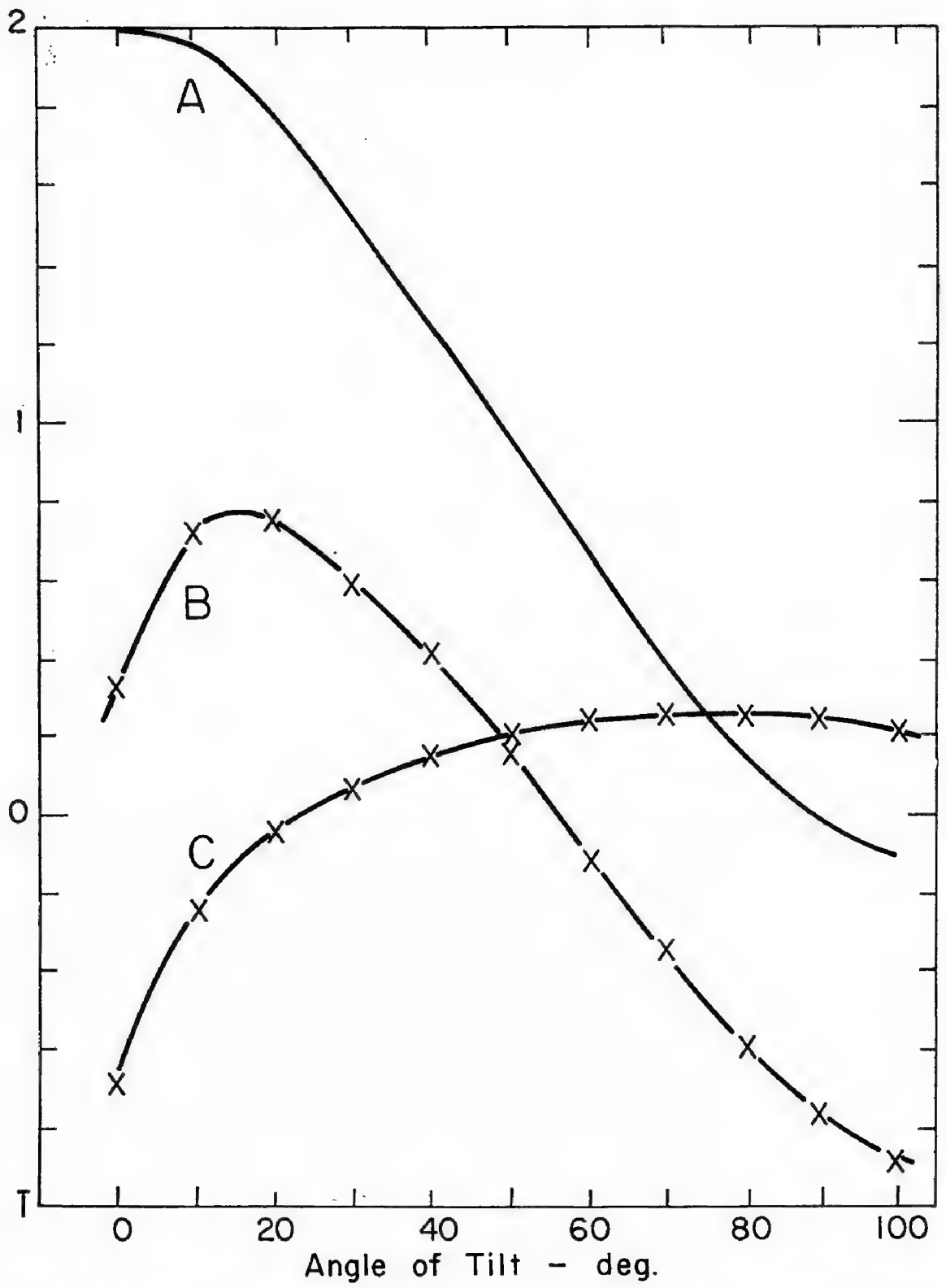
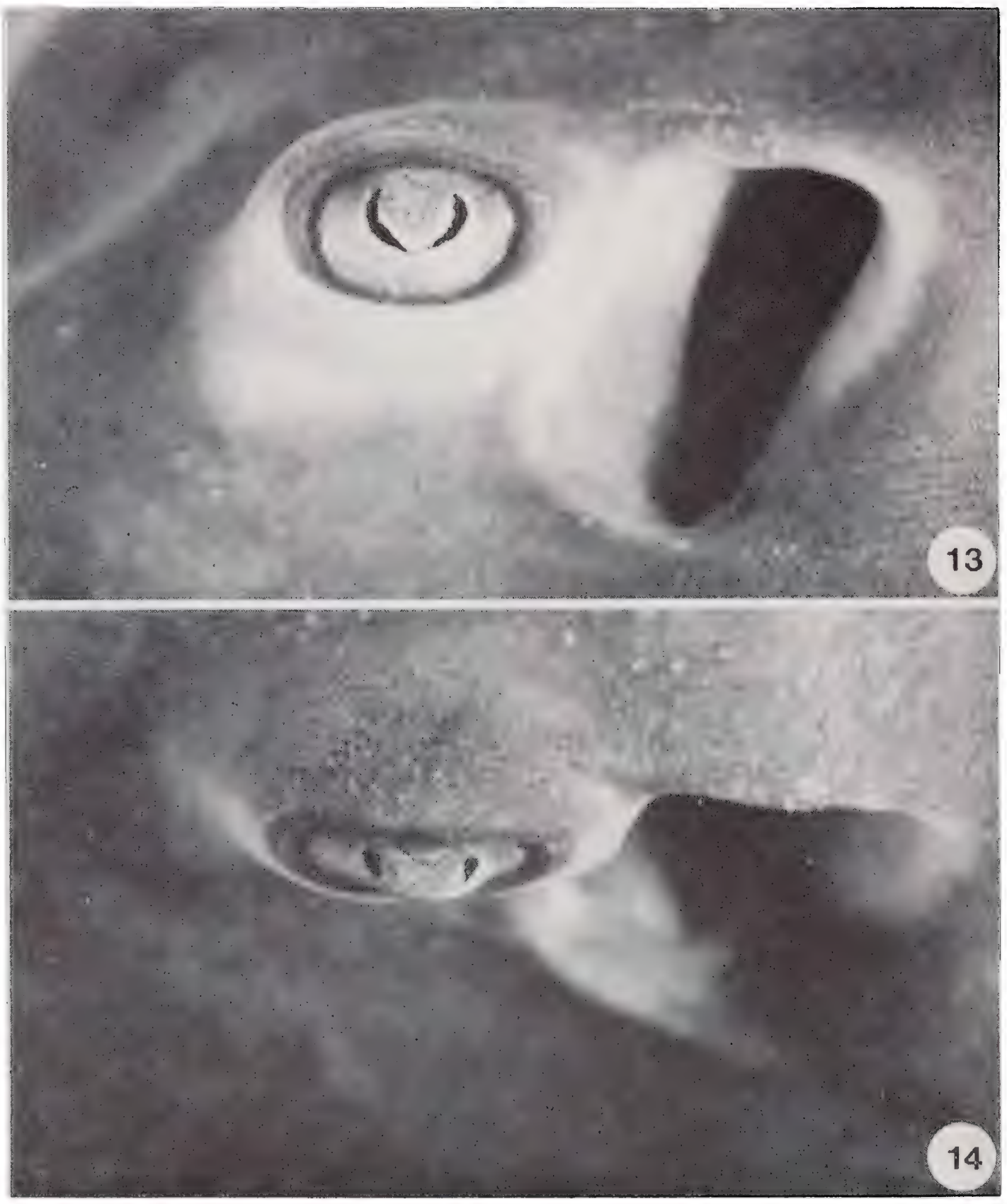


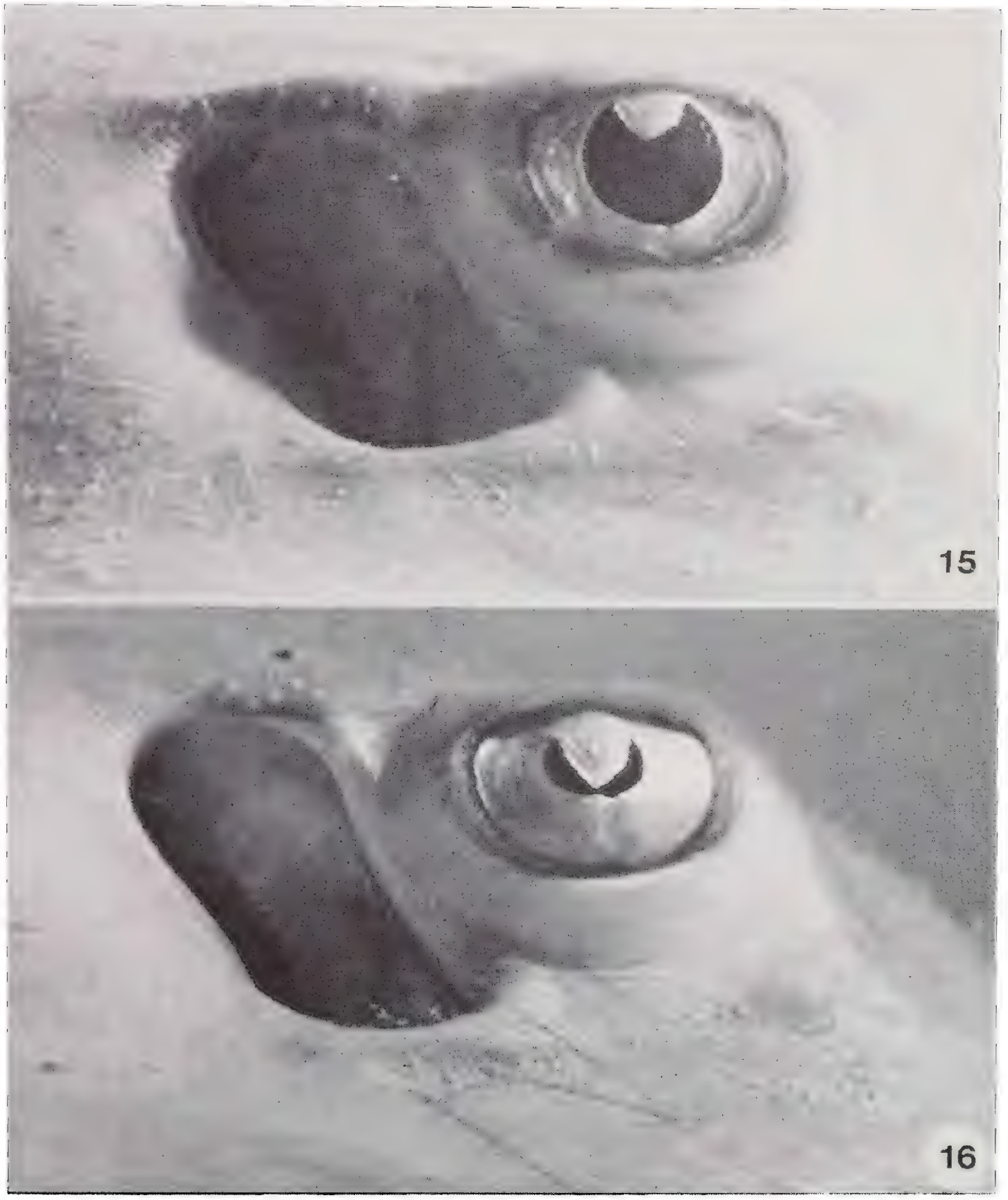
FIG. 12. A diagram illustrating the distribution of submarine irradiance (zenith sun or overcast sky), pupillary areas presented to incident light at successive angles of tilt, and relative amounts of light on the eye from 0° to 100°. Values for distribution of submarine radiance generalized from data in Jerlov, 1968. Ordinates, log units. Curve A, radiance normalized at 0°. B, pupillary aperature, maximum at 80°, 1.84 mm². C, area of pupil × radiance (× 0.1).

frosted glass, is localized on the external surface, probably in the epithelium; it is easily removed by gently scraping the outside of the cornea, whereupon the tissue beneath is seen to be clear. Optical densities are low (0.05) throughout most of the visible spectrum, rising slightly in the far blue (Fig. 17).

The lens is usually colorless or faintly yellow. The optical density is low through most of the visible spectrum, rising steeply below 450 nm (Fig 17). A



FIGS. 13 AND 14. Photographs of light-adapted eyes of a stingaree at tilt angles of 82° and 2°, respectively. Disc length 22 cm. × 4.8.



FIGS. 15 AND 16. Eye of a stingaree, dark- and light-adapted respectively. The fish after 1 h in darkness (Fig. 15) was transferred to sunlight for ½ h (Fig. 16). × 7.

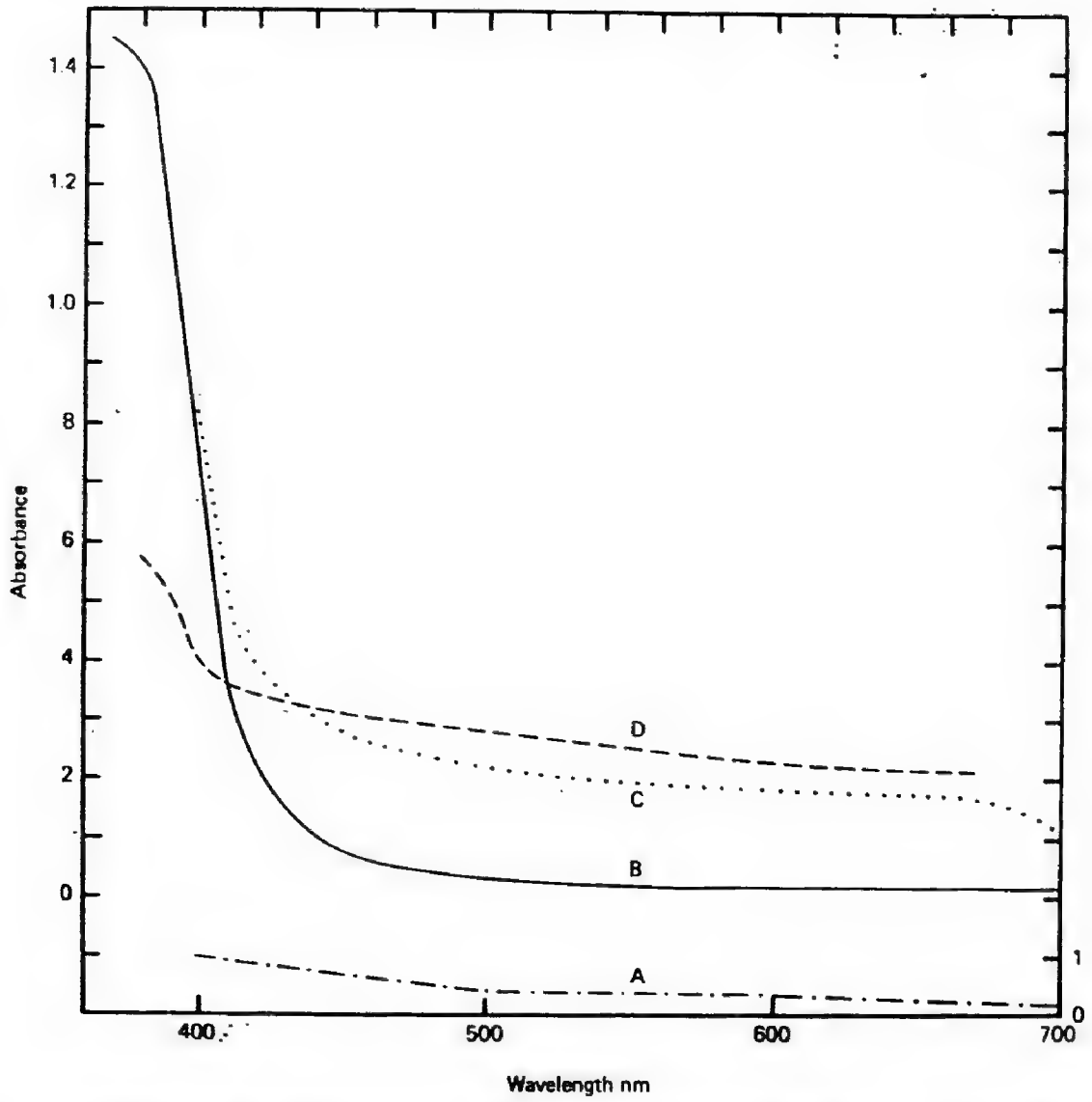


FIG. 17. Stingaree. Absorbance of the cornea (A), a colorless lens (B), a yellow lens from a large stingaree (C), and a homogenate of 20 lenses in Ringer (D). Scale for curve A to the right, for B, C and D to the left.

lens having a decidedly yellow cast was secured from a large stingaree; the spectrum curve (Fig. 17C) was similar to that of almost colorless lenses, but the density was higher. Absorbance of a homogenate of lenses rose steeply below 420 nm (Fig. 17D).

The absorbance of vitreous humor of the stingaree was least at long wavelengths, 0.02, and increased slightly below 500 nm, to 0.09 to 400 nm.

DISCUSSION

The cornea of the stingaree is equally transparent throughout the visible spectrum, but generally the external surface appears cloudy. This optical condition is produced by some peculiarity of the corneal epithelium. No systematic study has been made of the condition; it may be a response to abrasion ("sand-blasting") in the silt-laden shallow waters frequented by stingrays. The consequence must be to drastically reduce resolution.

The stingaree is a benthic animal and much of the time regards a water mass illuminated in a fairly regular and stable manner. Light in the sea tends to be

distributed fairly symetrically about the vertical (Tyler 1960); light entering the eye at 80° is 1/9th that entering at 0°. Relative intensities of light entering the L.A. pupil at successive angles of tilt from 0° to 100° are shown in Fig. 12.

The maximal angle for light entering the water is 48°, and to illustrate the range which may be encountered, an extreme case is taken of a radiance maximum at 23°, with the eye in the plane of maximal illumination (Table 1). From angle of tilt 80° to 23°, radiance increases 17 times, and light entering the eye increases 9 times. For these conditions, therefore, the pupil by its arrangement reduces light entering the eye to one-half.

The arguments presented above apply to fish well off the bottom. However, the photic conditions near the bottom in shallow waters are certainly different because of reflection of light upwards from the substratum (Jerlov 1968). The relative amounts of light entering the pupil over its vertical range of acceptance are altered accordingly.

When the pupil of the stingaree closes the amount of light entering the eye is reduced to one-fourth. Now, between noon daylight and twilight the stingaree may experience maximal changes of intensity of 6 orders of magnitude above the threshold for photopic vision, and reducing the pupillary aperture is obviously not effective in shielding the rods from high levels of illumination. In this respect the iris of the stingaree is less effective than that of some other animals; in the human eye, for example, pupillary aperture can be reduced to one-sixteenth of the maximum (Southall, 1973); in the gecko, to one three-hundredth (Denton 1956a).

The lenses of many fishes absorb short wavelengths, indeed yellow lenses are common among teleosts. The cut-off point for the lens of the stingaree *Dasyatis sabina* is 412 nm (the cut-off point is the wavelength at which the lens transmits 0.3 log units less that at 550 nm). In contrast, the cut-off point for the smooth hound *Mustelus canis* is 320 nm (Denton 1956b; Muntz 1972, 1973).

ACKNOWLEDGMENTS

Research support from NIH grant No. EY 00495 is acknowledged. Timothy Bechtel is thanked for doing the statistical analysis. Observations on eyes of deep-sea selachians were made in the Bay of Biscay on board R/V Sarsia of the Marine Biological Association (U.K.). The fish were caught by Mr. G. R. Forster on long lines, and he is thanked for permission to work on his specimens.

TABLE 1

Table illustrating the relative amounts of light entering the L.A. pupil normal to the plane of maximal illumination, when the latter occurs at angle of tilt 23°

Angle of tilt	Radiance J_R (relative)	Area of pupil A	J_RA
0	54.9	0.21	11.4
23	100	0.95	95
54	33.1	1.62	53.2
80	5.75	1.84	10.6
90	2.88	1.79	5.2

LITERATURE CITED

DENTON, E. J. 1956a. The responses of the pupil of *Gekko gekko* to external light stimulus. *J. gen. Physiol.* **40**:201–216.

————. 1956b. Recherches sur l'absorption de la lumière par le cristallin des poissons. *Bull. Inst. océanogr. Monaco.* **1071**:1–10.

GRUBER, S. H. 1967. A behavioral measurement of dark adaptation in the lemon shark *Negaprion brevirostris*. *In* P. W. Gilbert, R. F. Mathewson and D. P. Rall (eds.), *Sharks, Skates* and *Rays*, pp. 479–590. The Johns Hopkins Press, Baltimore, Maryland.

JERLOV, N. G. 1967. *Optical Oceanography*, Elsevier Publishing Co., Amsterdam, London, New York. 194 p.

KUCHNOW, K. P. and P. W. GILBERT. 1967. Preliminary *in vivo* studies on pupillary and tapetal pigment responses in the lemon shark, *Negaprion brevirostris*. *In* P. W. Gilbert, R. F. Mathewson and D. P. Rall (eds.) *Sharks, Skates* and *Rays*, pp. 465–477. The Johns Hopkins Press, Baltimore, Maryland.

MUNTZ, W. R. A. 1972. Inert absorbing and reflecting pigments. *In* H. J. A. Dartnall (ed.) *Handbook of Sensory Physiology*, VII/1, pp. 529–565. Springer-Verlag, Berlin, Heidelberg, New York.

————. 1973. Yellow filters and the absorption of light by the visual pigments of some Amazonian fishes. *Vision Res.* **13**:2235–2254.

NICHOLLS, J. V. V. 1933. The effect of temperature variations and of certain drugs upon the gastric motility of elasmobranch fishes. *Contr. Can. Biol.* **7**:477–463.

SOUTHALL, J. P. C. 1937. *Introduction to Physiological Optics*. Dover Publications, New York.

TYLER, J. E. 1960. Radiance distribution as a function of depth in an underwater environment. *Bull. Scripps Instn. Oceanogr. Univ. Calif.* **7**:363–412.

YOUNG, J. Z. 1933. Comparative studies on the physiology of the iris. I. Selachians. *Proc. Soc. B.* **112**:228–241.

LOW-FREQUENCY REVERSALS OF NEARSHORE CURRENTS IN THE NORTHWESTERN GULF OF MEXICO[1]

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ABSTRACT

Sub-surface current time series from a midwinter and a midsummer period are used to describe features of the near shore circulation in the northwestern Gulf of Mexico occurring over time scales of a few hours to a few weeks. Both time series show small tidal or inertial motions superimposed onto longer-period reversals in the nearshore flow, especially in the slower summer currents. At periods greater than about 45 hours, the coherence between the longshore component of the current and the longshore component of the computed wind-stress is significant at the 99% confidence limit for both study periods.

INTRODUCTION

Circulation patterns for the inner shelf waters of the northwestern Gulf of Mexico are based largely on a continuing series of drift bottle studies. Results reported by Watson and Behrens (1970) and Hunter, *et al.* (1974) indicate a generally southerly motion in winter and northerly currents in summer, though there may be significant departure from this pattern when surface winds vary from normal seasonal patterns. Broad features of the surface current patterns can be explained quite well in terms of seasonal wind systems.

Recording current meters have seen increasing use in the northwestern Gulf of Mexico, as elsewhere, in studies designed to investigate shorter-period variations, as well as the sub-surface motion not revealed by the drift bottle studies. A pilot study was initiated in 1973 along the inner shelf off the central Texas coast (Fig. 1) to investigate temporal variability in shelf circulation. Current meters were placed approximately ten kilometers offshore for two periods of just over a month each in the winter and summer of 1973 (Smith 1975). Results showed a quasi-steady flow to the south-southwest during the winter period. A series of low-frequency reversals characterized the summer data. The same general sampling pattern was repeated the following year to determine the extent to which the seasonal patterns recorded the first year were repeated. Results of

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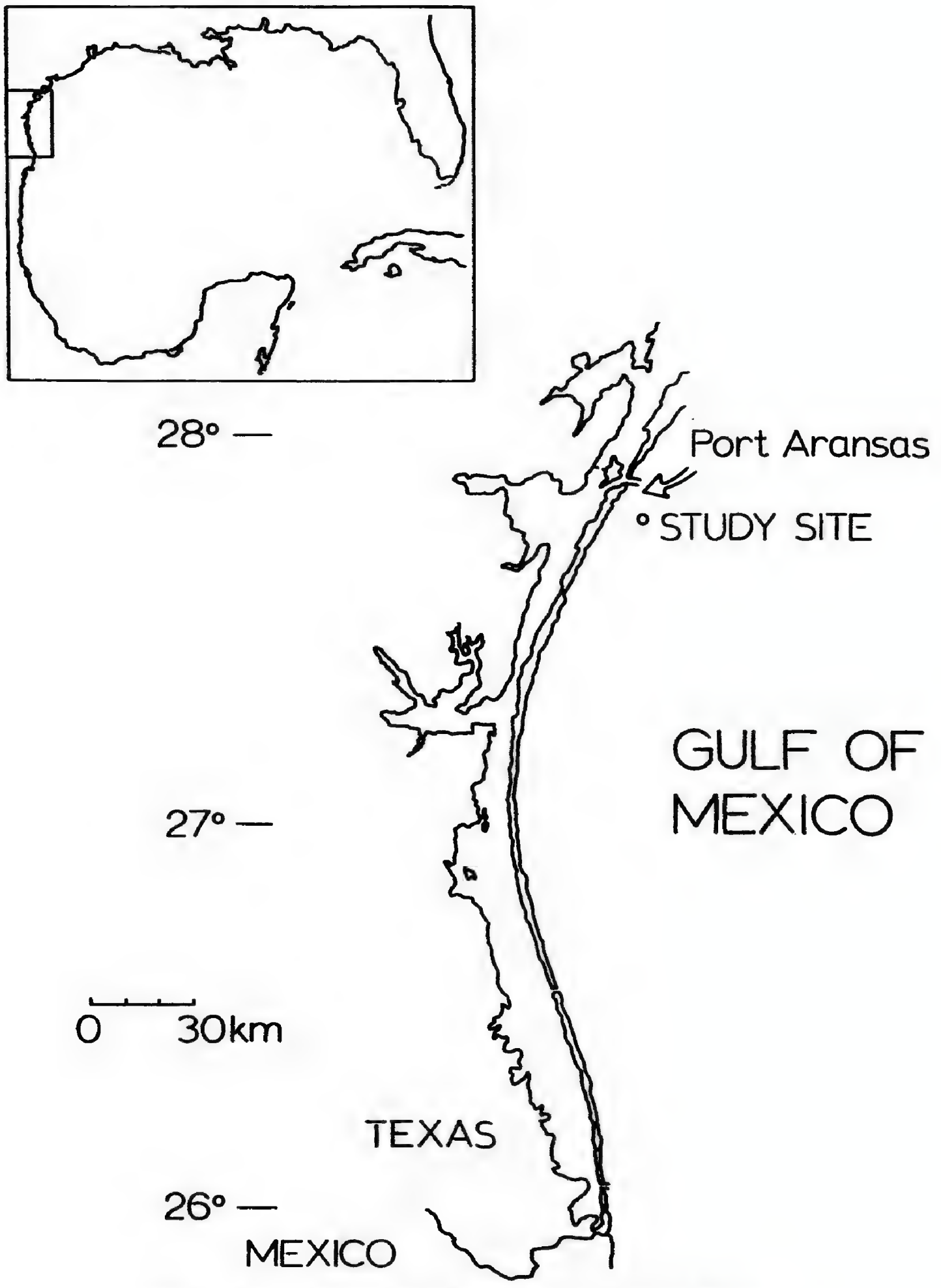

FIG. 1. Location of study site in the northwestern Gulf of Mexico.

the second year's study are presented here. The purpose of this paper is to describe the low-frequency variations characteristic of the inner shelf waters of the central Texas coast, and to obtain a quantitative relationship between reversals in the longshore component of the current and the low-frequency variations in coastal winds.

THE OBSERVATIONS

Half-hourly current measurements were made with an Environmental Devices Corporation Type 105 recording current meter, which provides time-integrated current speeds and directions over each sampling period. Currents were recorded at the 14 meter level on a taut-line mooring in 18 meters of water.

The first sampling period was a 49 day, 18.5 hour period from 21 November 1973 to 19 January 1974. The second time series was a 31 day, 16 hour interval from 18 June through 20 July 1974. Both winter and summer data were obtained approximately 10.5 kilometers off Port Aransas, Texas (Fig. 1). Isobaths closely parallel the coastline near the study site; the local cross-shelf gradient is about 0.9 meter per kilometer.

Wind data were recorded at three-hourly intervals at the U.S. Coast Guard Station at Port Aransas. The anemometer location was slightly less than 2 kilometers from the coast, and approximately 12 kilometers from the study site.

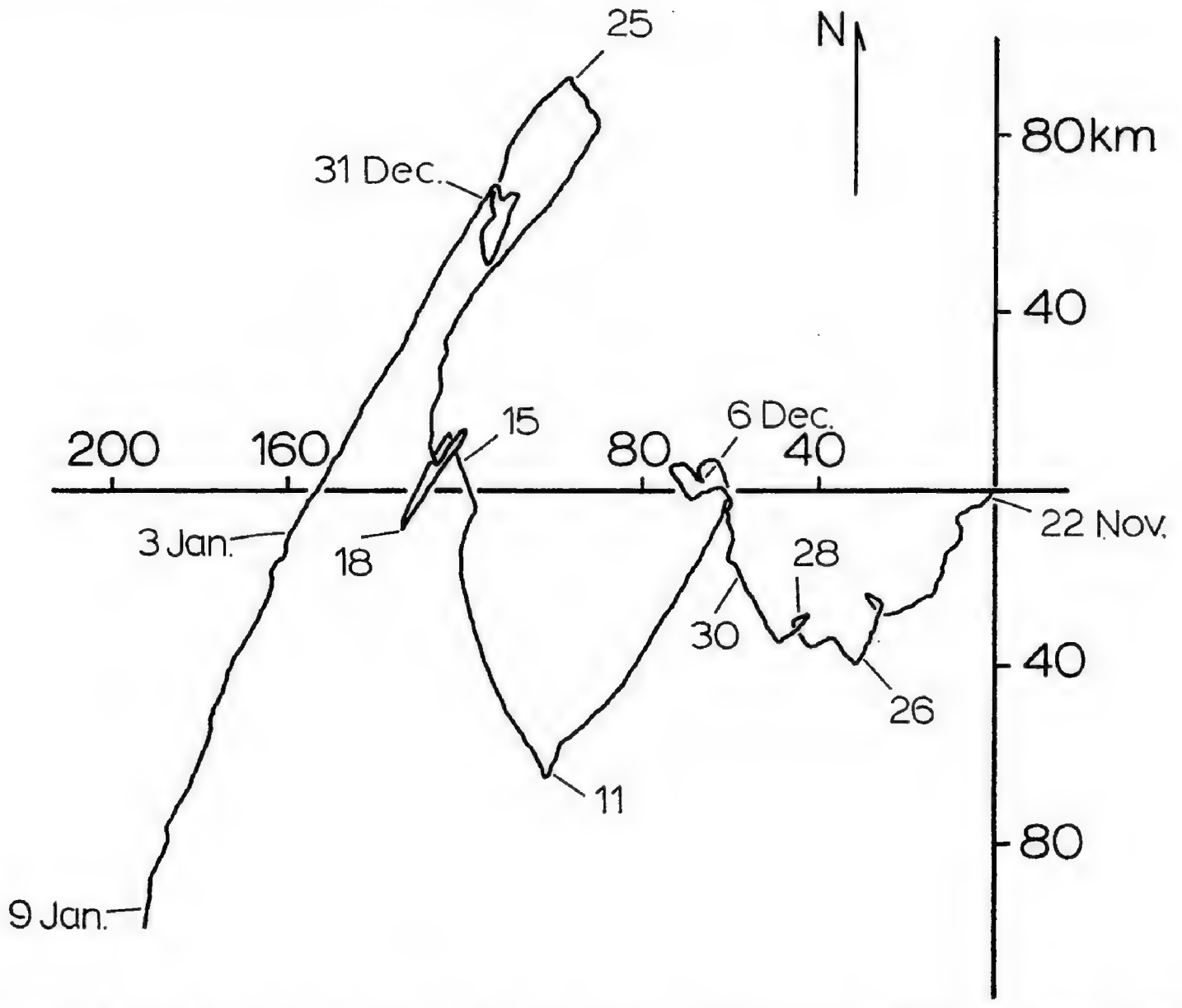

FIG. 2. Progressive vector diagram of sub-surface current vectors, 21 November 1973, to 10 January 1974. Calendar dates entered at 0001 CST.

RESULTS

The nearly fifty days of winter current data indicate an alternating nearshore current (Fig 2), with reversals occurring irregularly over time intervals on the order of a week. Shorter period variations, apparently poorly developed tidal or local inertial period (25.8 hours) oscillations, occur in late November and again in mid December. The proximity of the coastline tends to inhibit complete rotations in the tidal and inertial current components.

An interesting feature of the nearshore motion involves the cross-shelf component of the current vector. Currents moving to the south-southwest very nearly parallel the coastline and the 18 meter isobath at the study site (035°–215°).

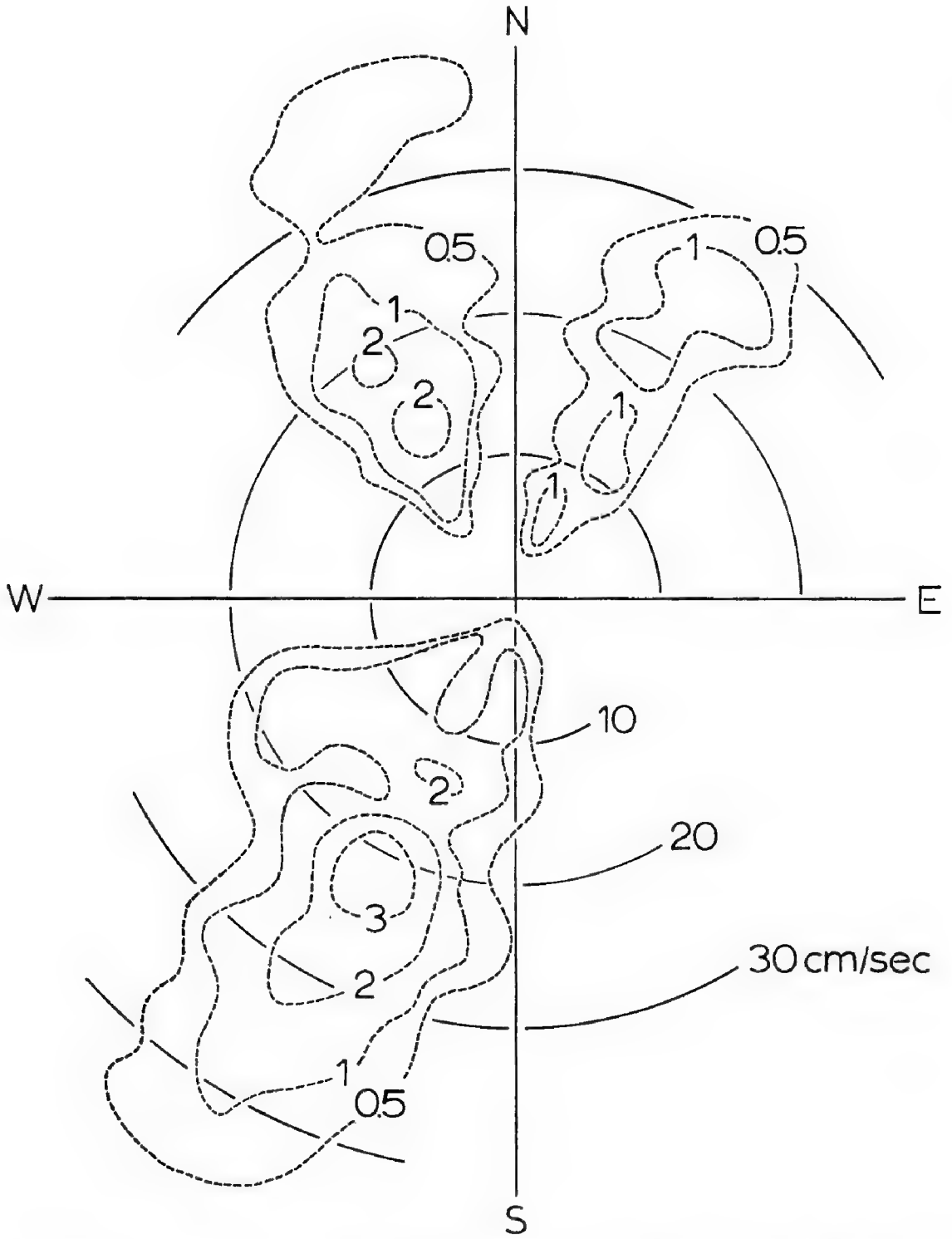

FIG. 3. Vector frequency diagram for sub-surface currents, 21 November 1973, to 10 January 1974. Frequency isopleths in percent.

Following a reversal in the flow, however, a definite onshore component appears, deflecting an otherwise longshore current into the northwest quadrant. Thus, the progressive vector diagram takes on an uneven, zig-zag appearance, heading alternately into the northwest and southwest quadrants. The resultant current vector for this time interval has a heading of 243° and a speed of 5 cm/sec.

A vector frequency diagram was constructed by expressing the total number of current vectors falling in each block of a 3 cm/sec by 10° grid as a percent of the total (Fig. 3). The result shows a concentration of current vectors with headings between 200° and 210°; however, substantial numbers of observations are indicated between 190° and 230°, or about 20° on either side of a direction parallel to the coast. When the current reverses, motion is concentrated along two headings, with maxima occurring between 320° and 330°, indicating an onshore

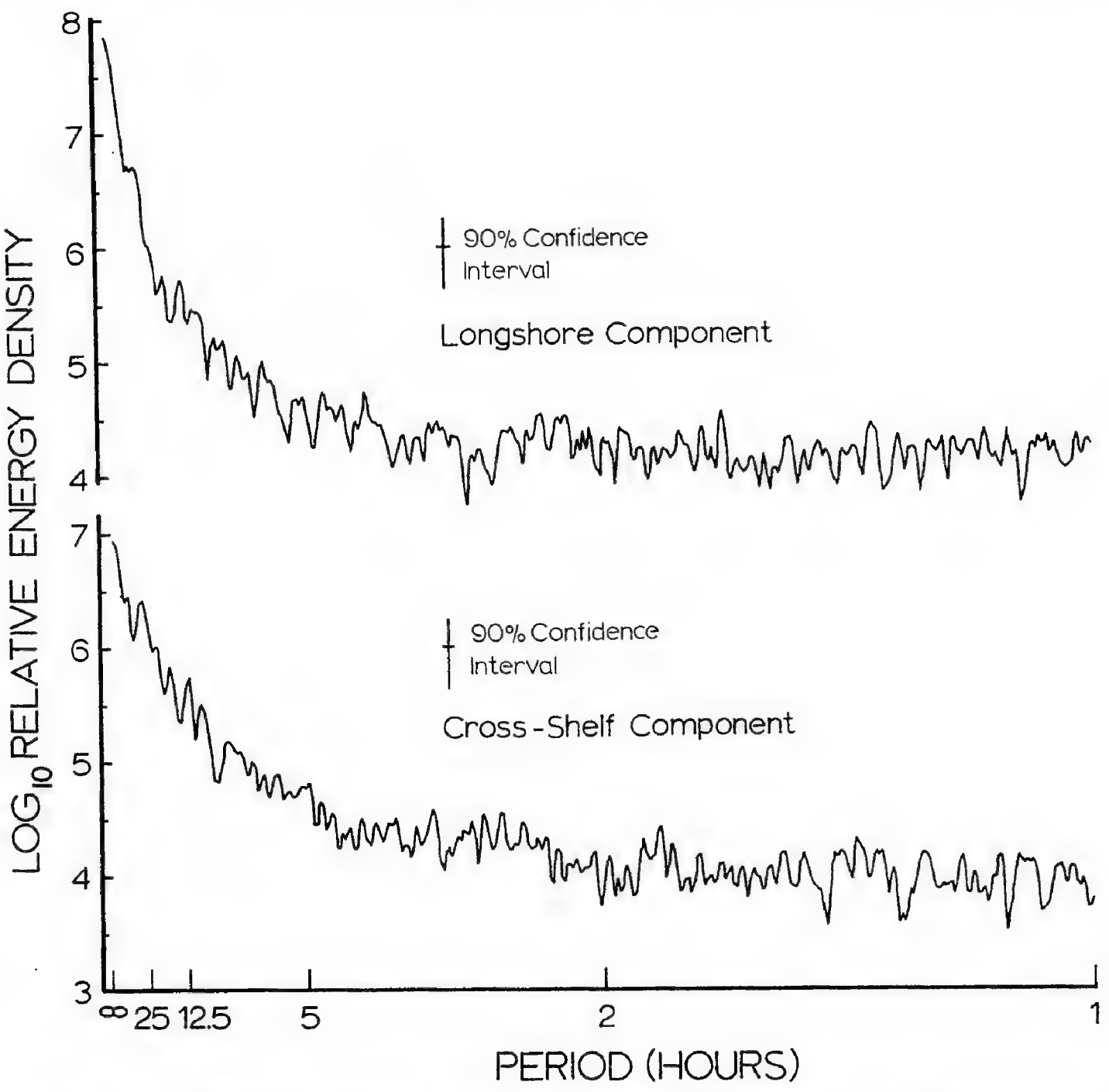

FIG. 4. Energy density spectra of longshore and crossshelf component current data, 21 November 1973, to 10 January 1974. Vertical axis in $(cm/sec)^2$/cycle per hour. Spectral resolution is 0.0029 cph.

component. All currents enclosed by the 0.5% isopleth are less than 45 cm/sec. Highest frequencies are found at speeds of between approximately 15 and 25 cm/sec.

Energy density spectra were computed after the raw current vectors had been decomposed into longshore (033°–213°) and cross-shelf (123°–303°) components. The computation used a fast-Fourier transform technique (Fee 1969) after the linear trend had been removed from the time series. The results are shown in Figure 4. Neither spectrum indicates statistically significant peaks at the diurnal or semi-diurnal tidal periods. This is in agreement with the low tidal

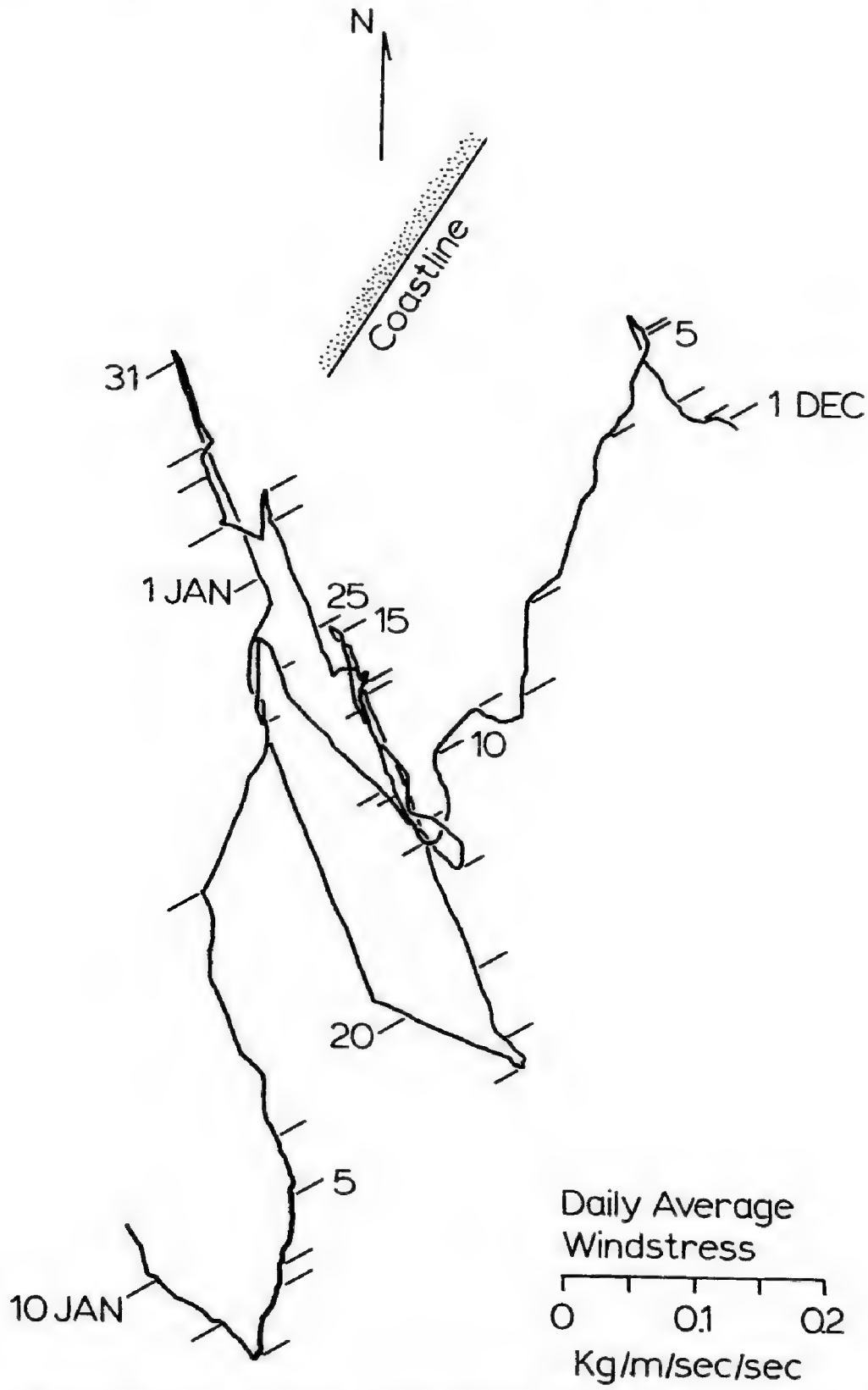

FIG. 5. Progressive vector diagram of three-hourly surface windstress vectors, 20 November 1973, to 10 January 1974. Calendar dates entered at 0001 CST. Winds measured at Port Aransas.

amplitudes characteristic of the northwestern Gulf of Mexico (Zetler and Hansen 1970) and underlines the relative importance of the long-period motions. The principal difference between the two spectra lies in the computed energy levels at the longest periods. The alternating nature of the nearshore current increases the long-period energy density levels of the longshore components to approximately an order of magnitude above those computed from the cross-shelf components.

The contribution to the observed current by the principal diurnal and semidiurnal tidal constituents was further invetigated by a harmonic analysis of the longshore and cross-shelf current components (Dennis and Long 1971). Computed amplitudes for all constituents are less than 2.0 cm/sec. This is not felt to be significant in view of the ± 5.9 cm/sec precision of the current meter.

The progressive vector diagram of the computed windstress vectors during the winter study is shown in Figure 5. Windstress vectors were computed using the expression $\tau = \rho C_d|V|V$, where V is the three-hourly wind velocity vector. The air density, ρ, and the drag coefficient, C_d, were assumed constant with values of 1.23 kg/m^3 and 0.0013, respectively, The resultant windstress vector is directed along a heading of 216°, which is very nearly parallel to the local longshore direction of 033°–213°. The progressive vector pattern, however, is composed of a series of reversals, occurring in response to frontal passages. These fronts are indicated by a shift to winds out of the northern quadrant on 4, 15 and 31 December. Strongest winds are generally recorded within the first two days following each frontal passage. Strongest south-southeasterly winds are recorded on 23 December.

The response of the longshore component of the current to the longshore component of the wind was investigated by computing a coherence spectrum (Fee 1969) from the winter data. Results are summarized in Table 1. Coherence values

TABLE 1

Low-frequency coherences for longshore current components and longshore components of the computed windstress

a. Winter Study. 1 December 1973 through 9 January 1974. 99% confidence limit is 0.52

Frequency (cph)	Coherence
0.000	0.85
0.004	0.77
0.008	0.73
0.012	0.65
0.017	0.54
0.021	0.69
0.025	0.74
0.029	0.51

b. Summer Study. 19 June through 19 July 1974. 99% confidence limit is 0.51

Frequency (cph)	Coherence
0.000	0.81
0.006	0.80
0.011	0.77
0.017	0.75
0.022	0.72
0.028	0.50

significant at the 99% confidence level were computed at periods greater than 40 hours (0.025 cph). While the low-frequency variations in the longshore current appear to be wind-driven, the nature of this air-sea coupling awaits a more detailed investigation.

The progressive vector diagram for the summer current data (Fig. 6) is characterized by a single major reversal; however, there is a substantial amount of shorter-period variability superimposed onto this pattern. Early in the record, there are approximately six days of little net motion, during which several tidal or inertial rotations dominate the pattern. Strong currents to the southwest start on 24 June and continue for the next six days, until an abrupt reversal in the nearshore flow begins moving water back to the northeast. The net motion during this nearly 32-day time interval is approximately westerly (277°) at 0.9 cm/sec.

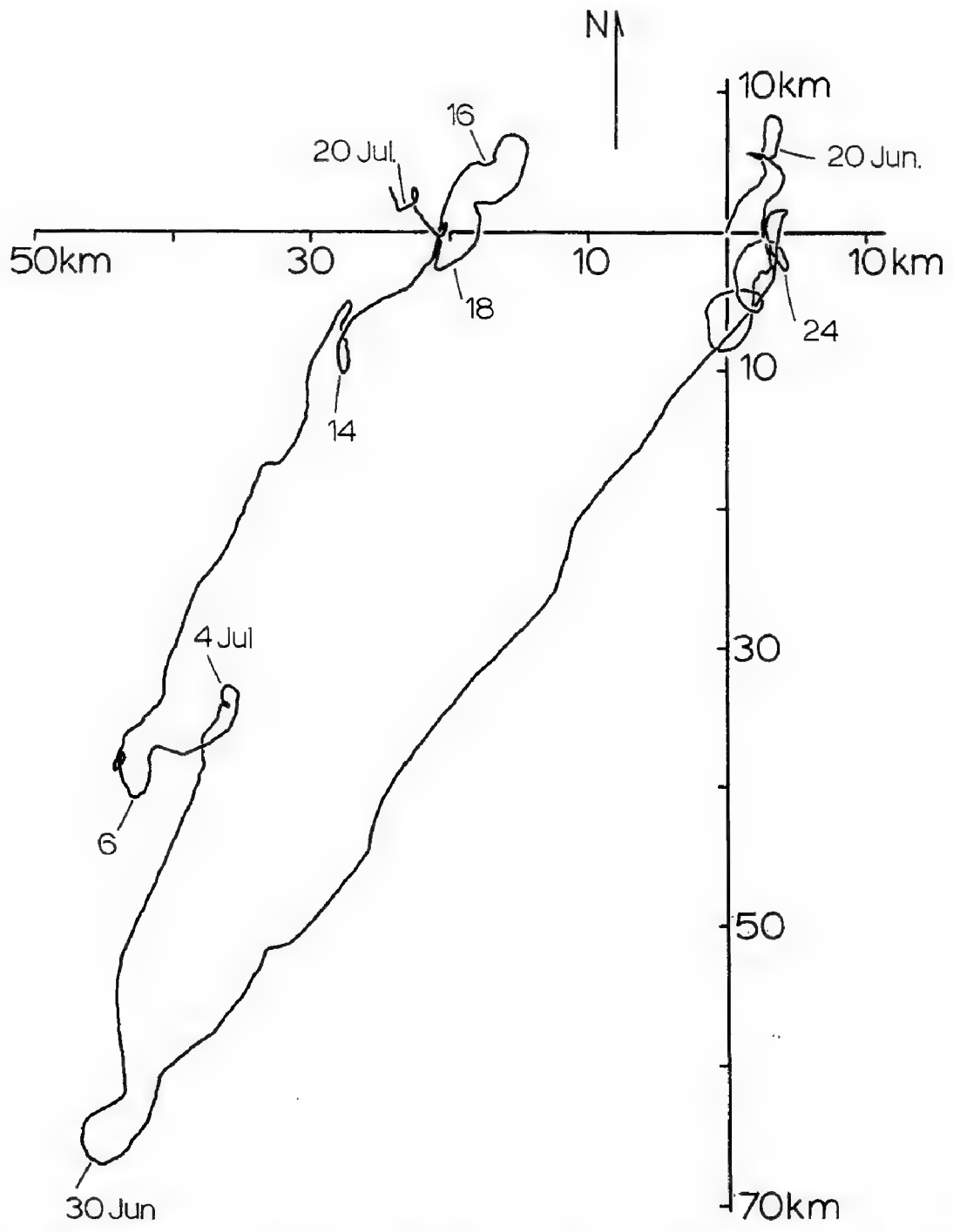

FIG. 6. Progressive vetor diagram of sub-surface current vectors, 18 June to 20 July 1974. Calendar dates entered at 0001 CST.

As in the winter data, the resultant flow poorly represents the instantaneous current recorded during the study period. It becomes apparent that the time-averaged current patterns provided by drift bottle data mask a substantial amount of temporal variability occurring over time scales ranging from a few hours to a few weeks.

The vector frequency diagram for the summer current data (Fig. 7) shows an essentially bimodal pattern, with highest frequencies between 020° and 040°, and over a broader arc between approximately 200° and 230°. Somewhat slower currents are recorded during the summer data. All currents within the 0.5% isopleth are less than approximately 30 cm/sec; highest concentrations occur at about 10 cm/sec toward the northeast.

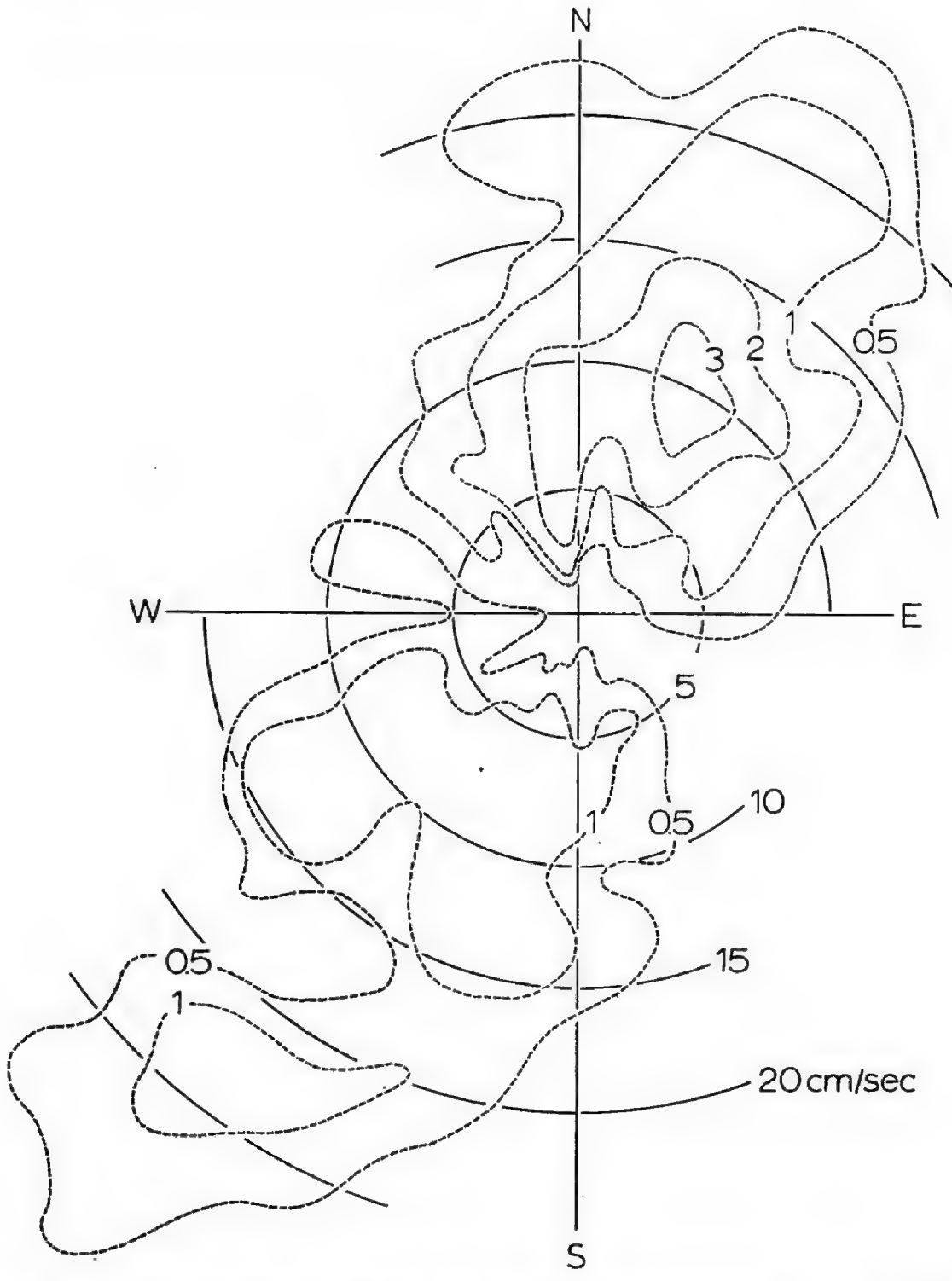

FIGURE 7. Vector frequency diagram for sub-surface currents, 18 June to 20 July 1974. Frequency isopleths in percent.

Both energy density spectra computed from the summer data (Fig. 8) show a small but distinct rise in energy density levels at approximately diurnal periodicities. In the cross-shelf component spectrum, the diurnal period peak stands over half an order of magnitude above surrounding energy levels, due to the absence of substantial cross-shelf motion at the longest periods. The spectrum computed from the longshore components shows long-period energy density values over one and a half orders of magnitude higher than those computed from the cross-shelf components at the same periods. Spectral peaks at periods of less than 24 hours are not felt to reflect physical processes.

The harmonic constants of the principal tidal constituents were computed for both longshore and cross-shelf current components. Amplitudes are somewhat larger than those computed for the winter data, but still well within the precision of the current meter, and thus not considered physically meaningful. The long-

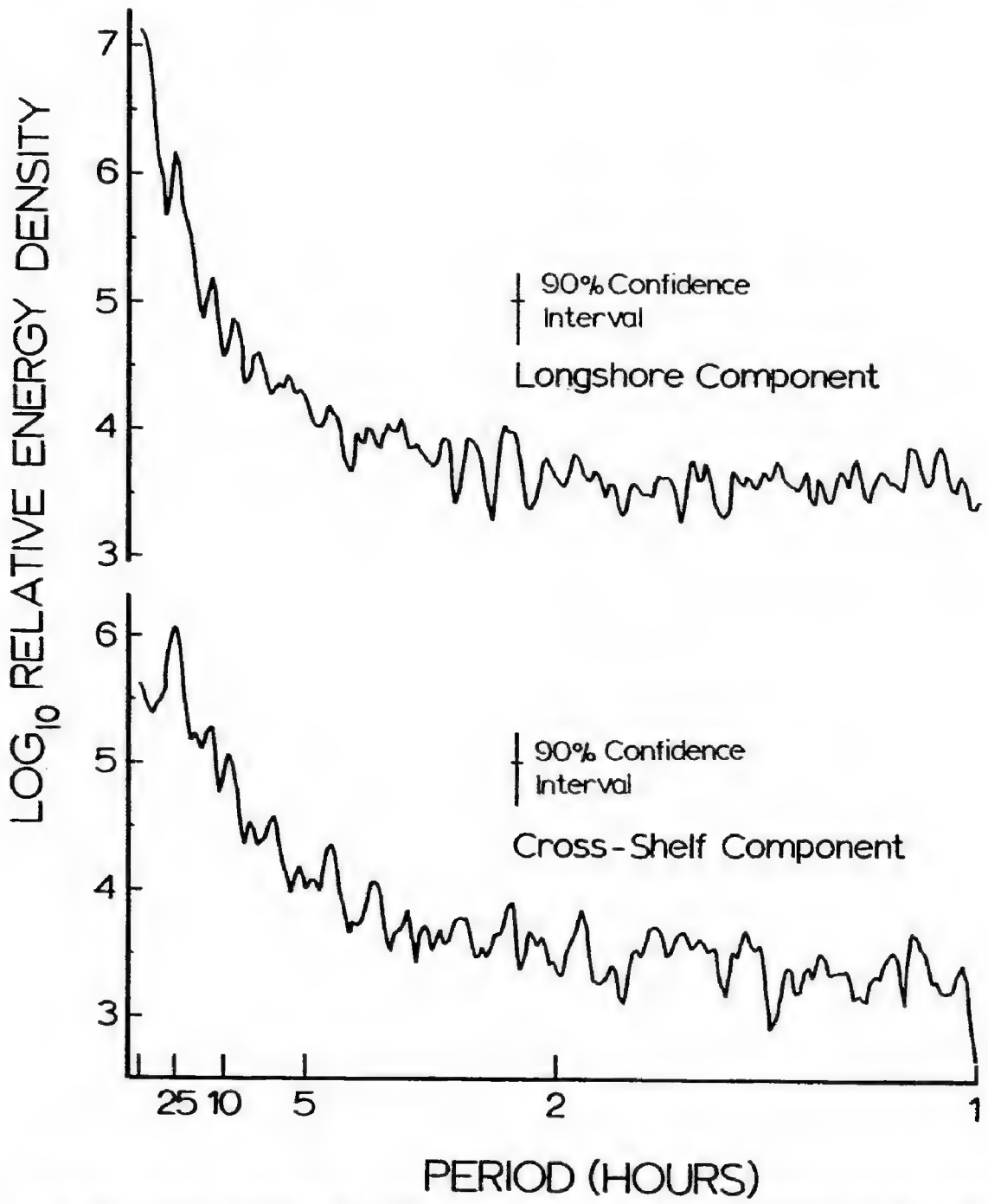

FIG. 8. Energy density spectra of longshore and cross-shelf component current data, 18 June to 20 July 1974. Vertical axis in $(cm/sec)^2$/cycle per hour. Spectral resolution is 0.0050 cph.

shore and cross-shelf components of the K_1 constituent were found to be 2.7 and 2.6 cm/sec, respectively.

The progressive vectors of the computed windstress vectors for the summer study are shown in Figure 9. The resultant vector for the entire 31½ day study interval is directed toward 305°, which is very nearly aligned with the local cross-shelf direction of 123°–303°. The pattern is characterized by two periods of quite steady, onshore winds, interrupted by about four days of northerly winds on 24 June. Strongest winds are only 33 km/hr (18 knots), recorded on 3 July. The coherence spectrum computed from the longshore current and windstress components recorded during the summer study (Table 1) shows statistically significant relationships at the 99% confidence level at periods longer than 45 hours (0.022 cph).

DISCUSSION

The two current time series described in this paper suggest that nearshore motion along the central Texas shelf may be characterized as an alternating, predominantly wind-driven current, with only a slight tidal or inertial component. Such tidal-period variations as there are should be interpreted with suspicion. In an earlier paper (Smith 1975), it was noted that tidal motions were greater in the cross-shelf components, which suggested they were only deflections in the longshore current produced by tidal exchanges throughout the nearby Aransas Pass (Fig. 1). Hydrographic data were not obtained as part of this study. However, available hydrographic data from inner shelf waters off Port Aransas (Smith 1976) indicate that strong density gradients are not normally present to

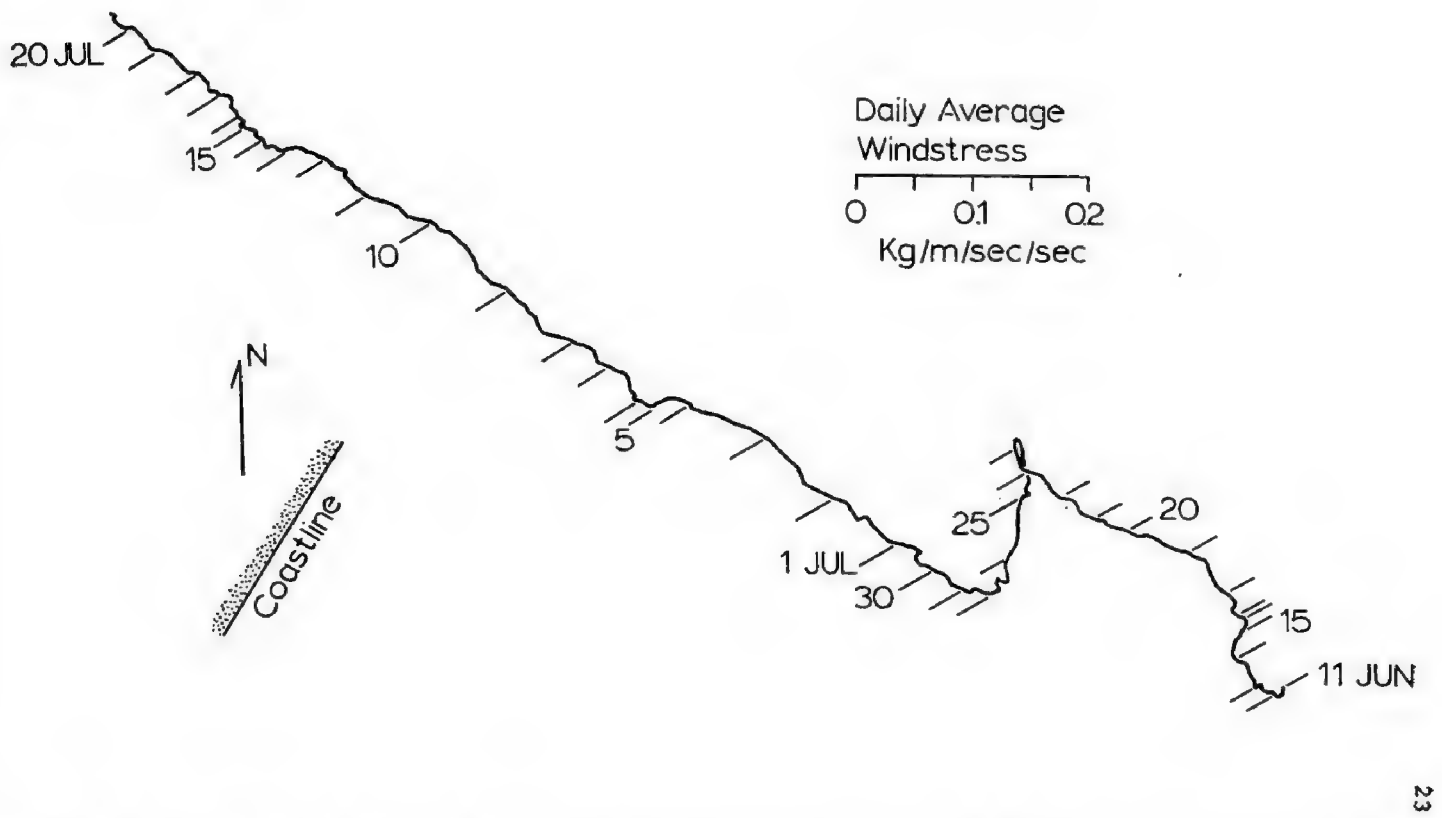

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FIG. 9. Progressive vector diagram of three-hourly surface windstress vectors, 11 June to 20 July 1974. Calendar dates entered at 0001 CST. Winds measured at Port Aransas.

drive a significant baroclinic current. In view of the relatively minor importance of rotary tidal or inertial motions, the lack of a permanent circulation system affecting these shelf waters, and an insignificant baroclinic contribution, the nearshore current must be almost exclusively wind-driven. The computed coherences between the computed windstress and current time series should be treated with caution, however, as the coupling of surface winds and sub-surface currents is undoubtedly more than a simple wind drift effect. The documentation of these driving forces awaits a substantially broader data base.

The data indicate a distinct shift to slower current speeds during the summer months, when speeds decrease to a median of around 10 cm/sec (Fig. 7). Also, the vector frequency diagram shows a greater frequency of currents to the north-northwest and north-northeast. The probable explanation lies in the seasonal shift in windstress vectors. The resultant windstress vector during the winter study is directed nearly parallel to the coast. In spite of the short periods when windstress was largely in the local cross-shelf direction, winds could be expected to generate and maintain longshore motion. The summer study was conducted during a time when the windstress vectors were quite persistently directed onshore. With significant longshore windstress components restricted to a four-day period in late June, little net motion in either longshore direction would be expected. Barotropic motion to the south-southwest might be started in response to the pressure gradient caused by water forced up against the coast, but this motion would be halted farther to the south along the curving coastline, as the nearshore current started to move upwind.

An interesting feature which cannot be resolved with the available data is the cross-shelf component of the flow recorded at the 14 meter level. While the kinematic boundary condition of the coast would inhibit cross-shelf motion, there does seem to be a persistent onshore component associated with the long shore motion to the south-southwest. This may have an important effect in restricting or enhancing the cross-shelf transport of suspended solids, planktonic populations, or whatever else might be unequally distributed through the water column. A cross-shelf component is not indicated for longshore motion to the north-northeast. The importance of the cross-shelf component of the nearshore motion makes this worthy of further study.

The comparison of these winter and summer time series with those described previously (Smith 1975) suggest that even broad seasonal patterns may not be repeated from one year to the next, but that year-to-year differences may be a result of the non-repetition of wind patterns.

Summer current patterns recorded in 1973 and again in 1974 were dominated by low-frequency reversals in the longshore motion occurring over time scales on the order of one to two weeks. During both summer study periods, coastal winds were persistently heading nearly directly onshore. Slight variations in a predominantly onshore wind can reverse the longshore component of the windstress and eventually reverse longshore motion, producing the observed alternating current.

The winter current patterns recorded in 1973 and in 1973–1974 are distinctly

different; however, the wind patterns recorded during these two study periods were also dissimilar. For most of the first three weeks of the 1973 winter study, windstress vectors were very nearly parallel to the local coastline and directed to the south-southwest. Late in the study period, winds decreased and were headed more directly onshore, though the longshore component of the windstress never reversed. This is consistent with the recorded current, which flowed nearly continuously to the south-southwest.

For the follow-up study conducted during the winter of 1973–1974, Figure 5 shows a resultant windstress vector which nearly parallels the coast; however, during the study period the longshore component of the windstress reverses six times. This is consistent with the observed sub-surface motion, which indicated four major reversals during the nearly 50-day study period. The high coherences computed at low frequencies (Table 1) support the conclusion that currents primarily reflect coastal wind patterns, which themselves may differ substantially from one year to the next.

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LITERATURE CITED

DENNIS, R. and E. LONG. 1971. A user's guide to a computer program for harmonic analysis of data at tidal frequencies. *NOAA Tech. Rept. Nos.* **41**, U.S. Dept. Comm., 31 pp.

FEE, E. 1969. Digital computer programs for spectral analysis of time series. *Spec. Rep.* Center for Great Lakes Studies, Univ. Wis. (Milwaukee). No. **6**, 17 pp.

HUNTER, R., G. HILL and L. GARRISON. 1974. Drift patterns along the South Texas coast, 1970–1973. *U.S.G.S. Misc. Field Studies Map*, **MF-623**, 2 sheets.

SMITH, N. 1975. Seasonal variations in nearshore circulation in the northwestern Gulf of Mexico. *Contr. mar. Sci.* **19**:49–65.

————. 1976. Hydrographic study of Texas outer continental shelf waters .*In*: Environmental Assessment of the South Texas Outer Continental Shelf, Chemical and Biological Component. Draft Report to the Bureau of Land Management for Contract 08550-CTS-17, pp. 13–46.

WATSON, R. and E. W. BEHRENS. 1970. Nearshore surface currents, southeastern Texas Gulf coast. *Contr. mar Sci.* **15**:133–143.

ZETLER, B. D. and D. V. HANSEN. 1970. Tides in the Gulf of Mexico—A Review and Proposed Program. *Bull. mar. Sci.* **20(1)**:57–69.

HABITAT ADAPTATIONS OF *ISOCHELES WURDEMANNI* STIMPSON (CRUSTACEA: ANOMURA: DIOGENIDAE) AND SEASONALITY OF OCCURENCES IN NORTHWESTERN FLORIDA

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ABSTRACT

Isocheles wurdemanni Stimpson seasonally occurs in the nearshore waters off high energy sand beaches in northwestern Florida. Peak occurrences are in spring (May–June) and fall (Sept.–Nov.) with maximum densities in the fall. Reproductive periodicity coincides with the spring and fall occurrences with 76.1% of females carrying eggs in the fall and 8.3% in the spring. Food is obtained by filtering wave-generated currents with the second antenna; particles as small as 25 μ are retained. The hermit crab is usually buried but is found on the substrate surface when feeding. Respiratory water currents are the same whether specimens are buried or are actively moving over the substrate. Currents are drawn from a water filled cavity maintained by the position of the gastropod shell upon burial. A preference for shells of *Thais floridana* Conrad is found, especially among ovigerous females (95.6% found in *Thais* shells).

INTRODUCTION

Although *Isacheles wurdemanni* Stimpson is mentioned occasionally in scientific papers (e.g., Fotheringham 1976, p. 570), reports concerned with its activities and adaptations are lacking. This may be due partially to the habitat, sand beaches with high wave action. Large seasonal populations of *I. wurdemanni* occur in the nearshore waters of northwestern Florida and studies were undertaken to determine the habitat adaptations of a hermit crab to a high wave action environment.

METHODS

Collections of hermit crabs $\geq$ 4 mm carapace length were made using skin diving techniques along the Gulf of Mexico beaches of St. George Island, Franklin Co., Florida. Samples were taken irregularly: during the fall and spring, collections were made at least every other week; during winter and summer, collections were made every 4–6 weeks. Preserved specimens were

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examined for appendage morphology, gastric mill anatomy, reproductive state, and shell preferences; living specimens were observed for feeding activities, burying mechanisms, and respiratory currents. Structural observations were conducted with the aid of a stereomicroscope on whole and dissected specimens. Field and laboratory examinations were made of feeding and burying activities while respiratory currents were traced in the laboratory. Field observations were conducted on the offshore sandbars in approximately 1 m of water with the aid of SCUBA techniques (additional weights were required to prevent excessive movement as a result of surge currents). Filtering ability was measured with the aid of sized diamond and silicon carbide particles and stomach contents were examined in 50 specimens. Respiratory current pathways were determined with the aid of carmine particles in a seawater solution or with methylene blue in seawater. A small amount of the stain solution was released from a pipet and subsequent particle/solution movements were observed. With buried hermit crabs, a pipet was introduced beside the crab, but release of the stain was delayed 10–15 min so that the initial withdrawal of *I. wurdemanni* had passed. Reproductive state was determined by removing the crabs from their shells and observing the sex and the presence or absence of attached eggs. Shell preferences were determined concurrent with sex.

HABITAT AND BURYING

More than 95% of a total of 756 specimens were captured during the spring and fall on the beach side of offshore sand bars (20–50 m offshore) or within 3 m of the splash zone along the sand beaches. Wave crests usuall break in these regions causing maximum vertical displacement of water and the sand substrate concommitant with the surge created by the passing wave. Densities reach 286/m^2 along the offshore bars during the fall months (Sept.–Nov.) but the shoreline densities seldom exceeded 1.0/m^2 during the same time period.

Populations were sparse in all locations during winter (Jan.–March) and summer (June–Aug.) (< 0.1/m^2) with densities either increasing or decreasing as the fall or spring maxima approach or pass. During the months of decreased densities, a few specimens were captured in deeper offshore waters, but usually within 1.0 km of shore.

Overall, only 13.9% of the sampled hermit crabs were male: 13.7% of the specimens captured in spring and fall were male (98 males and 619 females) and 17.9% of the specimens captured during the remainder of the year were male (7 males and 32 females). Of the 105 males captured ≥ 4 mm carapace length, only 6 were ≥ 6 mm while 584 of the 651 females were ≥ 6 mm carapace length. Maximum sizes of preserved specimens were 7.4 mm carapace length for males and 9.2 mm carapace length for females.

Burying in these sand habitats consists of creating a depression in the substrate and being covered by sand displaced by breaking waves and surge. Digging begins as the crab assumes a stationary position with the chelipeds anteriorly directed; the chela penetrating the substrata 3–4 mm. The first and second pair of walking legs are flexed so that the propodus and dactylus point posterolaterally and contact the substrata. Sand is pushed posterolaterally by the walking legs which reach underneath the shell on the recovery stroke. Such activity forms a depression with the crab and the carried shell in the center. Digging activity ceases when the depression is equal to the shell width (i.e., when the upper level of the shell is even

with the substrata). Shifting sand caused by wave and surge action then buries the hermit crab. Burial in substrates other than sand proved unsuccessful in the laboratory, but a depression was formed by the hermit crab in all tested substrates (mud-sand, sand, shell hash, pebble). In natural conditions, i.e., with surge currents, burial may have been achieved.

RESPIRATORY CURRENTS

Respiratory water currents of active *I. wurdemanni* pass into the branchial chambers through spaces between the walking legs and chelipeds and exit around the scaphognathite. Water pathways were observed to continue the same pattern with buried crabs due to the placement of the carried gasropod shell. The aperture of the shell faces the substrata so that a water filled space is maintained upon burial. It is from within the space that *I. wurdemanni* was observed to draw its respiratory waters.

FEEDING AND GASTRIC MILL

Food materials are usually acquired by passively filtering the wave generated water currents with the antennae. A pair of setae arise from the lateral margins of the flattened, ventral surface at the base of each flagellar article with each seta having regularly spaced setules along its length (Fig. 1). As a wave passes, surge currents pass water through the setae of the antennae; particulate matter is retained within the mesh of the setae. Particles as small as 25μ are retained. Due to setal arrangement and spacing between the lateral lines of setae, sand grains usually fall from the antennae after the wave passes. In the absence of wave activity (i.e., in the laboratory and presumably offshore) the antennae wave in circular paths similar to those described by Greenwood (1927) for *Stratiotes setosus*.

Active selectivity of particles does not occur at the antennae and all entrapped material is passed to the mouthparts. Either the right or left antenna is flexed ventrally and grasped by the third maxillipeds. The endopodites of the third maxillipeds are extended and moved medially, grasping the antenna with the carpus, propodus, and dactylus. As the antenna is withdrawn, material is transferred to the third maxillipeds. The third maxillipeds are then flexed ventrally and grasped by the endopodites of the second maxillipeds. After material has been concentrated on the second maxillipeds, the endopodites are flexed orally and brushed from proximal to distal by the first maxillipeds and maxillae.

Particle sorting occurs during material transfer from the third and second maxillipeds to the inner mouthparts. Particles larger than 250μ are not passed orally and usually fall ventrally between the second and third maxillipeds. As rejected particles pass ventrally, they are brushed by the merus and ischium of the second and third maxillipeds. Material adhering to the setae of the maxillipeds is concentrated on the dactyl of the third maxillipeds. Setae on the mouthparts are shorter and stouter than those found on the antennae, and the distal half of each seta is serrate.

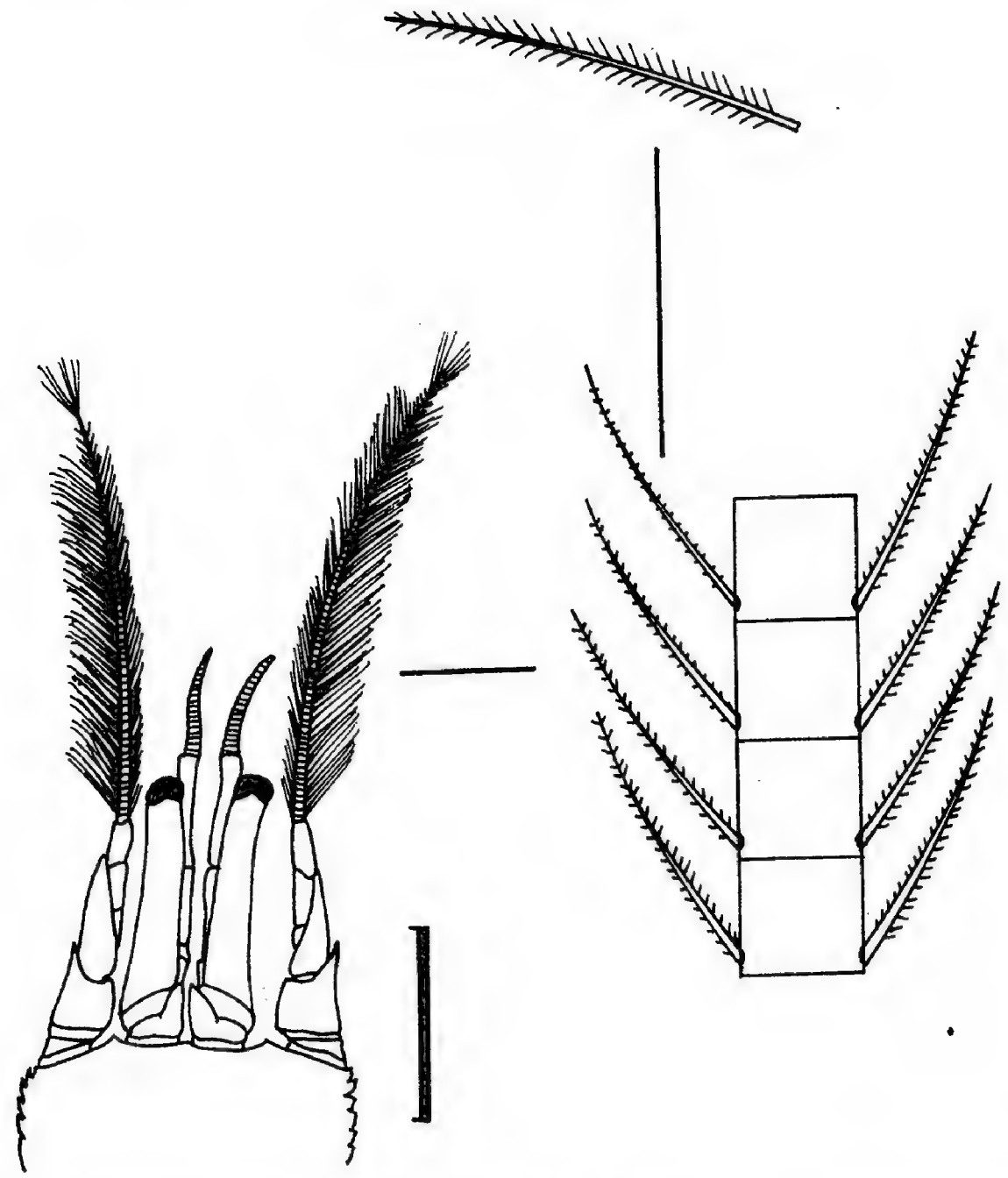

FIG. 1. Dorsal view of *Isocheles wurdemanni* with details of setal placement on the antennal flagellum and of the setae. Scale = 3 mm.

The gastric mill is composed of a simple median tooth, a pair of lateral teeth with eight small vertical ridges, and a cardio-pyloric valve with both teeth and setae. The median tooth lacks lateral ridges or wings and the anterior denticle of the lateral teeth is only slightly enlarged. Therefore, as the lateral teeth are passed by the median tooth, there is a crushing action.

Stomach contents consist of fine detritus and microscopic algae (95%) with sand grains (5%). Two unidentified copepods ($< 500\mu$) were found in the stomach of a large female, but other zooplankton were not present in the stomachs of the other specimens.

REPRODUCTIVE STATE

Ovigerous females were collected in May, June, Sept., Oct., and Nov., the time period that *I. wurdemanni* was collected in nearshore waters. Only 8.3% of fe-

TABLE 1

Seasonal occurrence and sexual distribution of *Isocheles wurdemanni* of carapace length > 4 mm. Numbers in parenthesis indicate the percentage of seasonal occurrence.

	May–June	Sept.–Nov.	Total
males	42 (17.9)	56 (11.6)	98 (13.7)
non-ovigerous females	177 (75.3)	102 (21.2)	279 (38.9)
ovigerous females	16 (6.8)	324 (67.2)	340 (47.4)
	235 (100)	482 (100)	717 (100)

males were ovigerous in the spring (May–June) but 76.1% were ovigerous in the fall (Sept.–Nov.). Although collections were made during other months, no ovigerous females were found (only 32 females and 7 males were collected). Lack of ovigerous females in other months may have been related to the number of specimens collected, but it may also reflect seasonal reproductive activity. The sexual distribution of the seasonal collections are listed in Table 1.

SHELL PREFERENCES

The occurrence of *I. wurdemanni* in identified gastropod shells is listed in Table 2. Weight index values were not determined as only preserved specimens were used in determining shell preferences. Collections of 265 sympatric living gastropods during the fall (coincident with the maximum *I. wurdemanni* population density) indicate that *Terebra dislocata* Say is the most common (62%), followed by *Oliva sayana* Revene (20%), *Thais floridana* Conrad (14%), and *Polinices duplicata* Say (4%). Only snails large enough to provide shells for adult *I. wurdemanni* were considered. Shell changing behavior by *I. wurdemanni* was observed on the offshore sand bars during periods of low wave activity, but dominance mechanisms were not determined.

DISCUSSION

Isocheles wurdemanni is adapted to high wave energy environments through its feeding and burying mechanisms. Morphological modifications are restricted to the antennae and setation of the appendages. The antennae are passive filters if wave and surge currents are present, but *I wurdemanni* is capable of actively

TABLE 2

Shell utilization of *Isocheles wurdemanni* considering sex and reproductive activity

	Male	Non-ovigerous Females	Ovigerous Females	Total
Thais floridana Conrad	14	143	325	482
Terebra dislocata Say	73	84	5	162
Oliva sayana Ravenel	0	29	8	37
Other	11	23	2	36
	98	279	340	717

filtering the ambient medium by waving its antennae in circular patterns if such currents are absent. Greenwood (1972), in laboratory observations of *Stratiotes setosus*, reported only active filtering. It is possible that field observations would include passive filtering for *S. setosus*.

Setation on the chelipeds and walking legs function in food acquisition. The setae are plumose and in contrast with the substrata. Small detrital material is trapped by these setae, gleaned through cleaning activities, and then ingested. Scavenging on dead macromaterial is probably minimal as such material is washed ashore by wave action.

Additional indications to the diet are found in the filtering apparatus of the gland filter of the gastric mill. Caine (1976) found the longitudinal bar spacing to be the least of six examined species of hermit crabs. (The porosity of the gland filter determines the size of particles passed to the hepatopancreas for digestion, those that pass through the filter, and the particles that are routed to the midgut, those too large to pass through the filter.) Therefore *I. wurdemanni* must feed on small material.

Respiratory water current pathways are the same whether the crab is active or buried. The dense setae on the basis of walking legs and mouthparts may partially filter water currents. Aquarium simulation of surge currents indicates that the water space within and immediately beneath the shell aperture of buried hermit crabs is not disturbed by surge activity. Such surge currents suspend sand grains on the surface of the substrata and filtration of respiratory currents may be more important when the hermit crab is active on the surface. On substrates other than sand, particularly very course substrates, respiratory currents of buried *I. wurdemanni* may require filtration of some small particles and the percolation of interstitial water through very fine substrates may preclude prolonged burial. However, neither situation was rigorously examined by field experiments.

Digging and burying mechanisms are similar for *I. wurdemanni* and *Pagurus longicarpus* (reported by Rebach 1974). Low temperatures initiated burying behavior of *P. longicarpus*, but *I. wurdemanni* regularly buried as part of its normal behavior. Rebach did not consider respiratory mechanisms of buried *P. longicarpus*, but they should be similar to those of *I. wurdemanni* as shell placement is similar.

The gastric mill of *I. wurdemanni* differs from other anomurans (Patwardhan 1935, Caine 1975). The median tooth is without lateral extensions and the vertical ridges are small. The urocardiac ossicle of hippids and porcellanids, also filter feeders, have minor dentations not found in *I. wurdemanni*, but the lateral teeth are similar. The major differences between *I. wurdemanni* and either hippids or porcellanids is found in the cardio-pyloric valve. The cardio-pyloric valve is either setose (Hippidae) or setose with minor ridges (Porcellanidae) for other examined anomuran filter feeders, but the cardio-pyloric valve is strongly toothed for *I. wurdemanni* (similar to *Clibanarius vittatus* Bosc, Caine 1975). The structure of the cardio-pyloric valve is indicative of the phylogenetic associations of *I. wur-*

demanni, as is the absence of ridges on the urocardiac ossicle, while the morphologies of the median tooth and lateral teeth are dietarily modified.

Sexual distributions may be the result of either sexually different habitat selection or a sexual size dimorphism. Only specimens ≥ 4 mm carapace length were used in this study, and the number of males decreased as size increased.

Size distributions are also evident in shell selection. Males occupied shells with small apertures (*Terebra*, Table 2). Ovigerous females occurred primarily in *Thais* shells (95.6%) whereas only 51.3% of the non-ovigerous females inhabited *Thais* shells. It is unclear if reproductive success is higher for females in *Thais* shells or if *Thais* shells are selectively acquired, or both. There are two possible explanations for the dimorphic sizes and shell preferences: either females are aggressively dominant and exclude males from larger shells, thereby restricting males to small sizes due to the availability of shells (hermit crab growth is generally accepted to be dependent upon shell availability), or, males are morphologically smaller than females and are not capable of inhabiting larger shells.

LITERATURE CITED

CAINE, E. A. 1975. Feeding and masticatory structures of selected Anomura (Crustacea). *J. exp. mar. Biol. Ecol.* **18**:277–301.

————. 1976. Relationship between diet and the gland filter of the gastric mill in hermit crabs (Paguridae). *Crustaceana.* **31**:312–313.

FOTHERINGHAM, N. 1976. Population consequences of shell utilization by hermit crabs. *Ecology.* **57**:570–578.

GREENWOOD, J. G. 1972. The mouthparts and behavior of two species of hermit crabs. *J. Nat. Hist.* **6**:325–337.

PATWARDHAN, S. S. 1935. On the structure and mechanism of the gastric mill in Decapoda. III. Structure of the gastric mill in Anomura. *Proc. Indian Acad. Sci.* **1B**:405–413.

REBACH, S. 1974. Burying behavior in relation to substrate and temperature in the hermit crab *Pagurus longicarpus. Ecology*. **55**:195–198.

THE DRIFT ALGAE COMMUNITY OF SEAGRASS BEDS IN REDFISH BAY, TEXAS[1]

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ABSTRACTS

Large quantities of drift algae found over seagrass beds in Redfish Bay, Texas showed net productivity and competed for light with the seagrasses. The biomass was very small compared to that of the seagrasses; however, it served as resources for animals and most importantly to reduce light over the seagrasses.

INTRODUCTION

The large quantities of unattached drift algae are a very striking feature of the seagrass beds of Redfish Bay, Texas. Drift algae accumulate almost knee-deep, especially over bare areas in the seagrass bed. Their large quantities, mobility, seasonality and ability to grow unattached have been noted (Isaac 1956; Phillips 1960, 1961; Conover 1964; Humm 1964).

The presence of a drift algae community in Redfish Bay and in certain bays of Florida (Phillips 1960, 1961) is fairly unique to Atlantic North America seagrass ecosystems dominated by *Thalassia testudium*. Intense herbivore pressure from reef fish and urchins such as *Diadema* may prevent drift accumulation in most of the subtropical and tropical *Thalassia* systems, as may the constant directional currents associated with the tradewinds of the Caribbean.

Seagrass ecosystems commonly export to the outside environments (Menzies, *et al.* 1967, Barsdate, *et al.* 1974). The drift algae of Texas grass beds perhaps represent the less common situation of outside environments importing to the grass beds.

Biomass and primary production of the drift algae community were measured in order to assess partially its role in the seagrass meadows of Redfish Bay.

MATERIALS AND METHODS

Field observations were made from 7 July to 30 August 1974 in Redfish Bay, Texas, primarily at two locations. These were the seagrass beds by Ransom Island (27°49′N and 97°8′W) and by the Fin and Feather Bait Shop (27°52′N and 97°8′W), near Port Aransas. Species present, rela-

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tive amount, and daily changes in the drift algae community was recorded. Taylor (1960), Wynne and Taylor (1973), and Edwards (1976) were referred to for taxonomy.

Biomass was collected by placing a wooden frame 34 × 38 cm with high sides over randomly-chosen sample areas in the grass beds and removing all drift algae inside the frame. Algae were sorted into dominant species, cleaned of detritus, blotted and weighed, dried at 90°C for 24 hr which gave constant weight, and weighed again.

Productivity was measured using a light and dark bottle oxygen technique (Strickland and Parsons 1965) and a radioactive carbon technique using 5μc of $NaH^{14}CO_3$ of known specific activity. Prior to incubation drift algae were removed from the seagrass bed, avoiding exposure to direct sunlight. Detritus was removed before algae were placed in glass-stoppered bottles. For each species duplicate light and duplicate dark bottles were used. Bottles incubated for 4 hr *in situ* for the O_2 experiments or in a trough exposed to natural sunlight and flushed with seawater for the ^{14}C experiments. The algae in the trough were no deeper than 5 cm. Following incubation using ^{14}C algae were removed from the bottles, wrapped in foil, and frozen immediately in the dark for subsequent dry combustion to release labelled CO_2. All algae were dried at 90°C for 24 hr and weighed.

One experiment determined the effect of light, measured as % of the surface irradiance (SI), on the rate of productivity, as estimated by ^{14}C uptake. Duplicate bottles incubated for 4 hr under a series of neutral density filters admitting 100, 73, 64, 41, and 0% SI.

Radioactive CO^2 released by combustion was trapped in scintillation fluid and measured in a Beckman LS-100C counter. Radioactive carbon uptake was calculated using the following formula:

$$P = \frac{DPM_{sample} \times 1.05 \times A \times V}{DPM_{available} \times T \times W}$$

where P = mg C·(g dry)$^{-1}$·hr^{-1}, DPM_{sample} = disintegrations per minute, corrected for quench, background, dark uptake, combustion efficiency, and scintillation counter efficiency, of oxidized sample, 1.05 = correction for differential uptake of C isotopes, A = alkalinity of water, mg C·l^{-1} (Strickland and Parsons 1965), V = volume of incubation bottle, l^{-1}, $DPM_{available}$ = activity of labelled bicarbonate added, disintegrations per minute, T = incubation time, hr, W = dry weight of algae, g.

Ml of O_2 were converted to mg O_2 and then to mg C by the formula 0.43 mg O_2 = X mg C. Instantaneous rates (mg C·(g dry)$^{-1}$) were converted to areal rates (g C·m^{-2}·day^{-1}) assuming a mean dry biomass and a 12 hr day.

RESULTS

Species composition (Table 1) remained fairly constant during the six weeks of observation. *Hypnea* spp. were the most common species. Incidental species appeared in the drift community for a week and disappeared. One such species was *Chaetomorpha linum* which at one time was very dominant and entangled other typical drift algae, holding them together in fist-sized balls. Seasonality of drift algae can be expected to reflect seasonality of the species comprising the community and weather, especially wind, conditions (Phillips 1961, Odum 1967, Edwards and Kapraun 1973).

Attached algae were very rare in the grass beds, suggesting drift algae originated outside the grass beds, probably on oyster reefs. The presence of *Grauteloupia* and *Soliera* also suggests import as the species do not grow in Redfish Bay (Edwards 1976). *Hypnea* spp. were the only drift algae, except for *Padina*, observed growing as epiphytes on the seagrasses during the study period. *Padina* grew on a submerged pipe and occasionally on *Thalassia*, but was rarely found

TABLE 1

Major species of drift algae from seagrass beds in Redfish Bay, Texas.

Division Chlorophycophyta
Chaetomorpha linum (Mueller) Kuetzing
Division Phaeophycophyta
Dictyota dichotoma (Hudson) Lamouroux
Padina vickersiae Hoyt
Division Rhodophycophyta
Digenia simplex (Wulfen) C. Agardh
Gracilaria debilis (Forsskål) Boergesen
Gracilaria foliifera (Forsskål) Boergesen
Gracilaria verrucosa..(Hudson) Papenfuss
Grateloupia filicina (Wulfen) J. Agardh
Hypnea cornuta (Lamouroux) J. Agardh
Hypnea musciformis (Wulfen) Lamouroux
Jania capillacea Harvey
Laurencia poitei (Lamouroux) Howe
Soliera tenera (J. Agardh) Wynne et Taylor

in the drift community. Seagrass epiphytes can break off and become drift algae, however many of the major species observed have not been recorded as seagrass epiphytes (Humm 1964, Ballantine and Humm 1975). The seagrass leaves allowed accumulation of the algae.

Drift algae attained a mean dry biomass of almost 200 g per m^2 (Table 2), which was only a fourth of the biomass of the seagrasses which yielded 795 $g \cdot m^{-2}$ (Topham, *et al.* 1975). The high variance associated with the biomass indicated drift algae had very heterogenous distribution over the seagrass beds. The algae accumulated most where seagrass growth was not well-developed such as in bare swaths cut by boat rudders or close to shore where seagrasses were desiccated upon exposure to air at lowtide. The drift community moved in and out of the grass beds with currents but moved little with tides.

Drift algae showed net productivity despite being composed in part of old or decomposing plants (Tables 3, 4). The mean contribution of 1.9 g $C \cdot m^{-2} \cdot day^{-1}$

TABLE 2

Biomass (wet and dry) of drift algae in Texas seagrass beds. Data represent 20 samples.

	g wet·m^{-2}		g dry·m^{-2}		
SPECIES	$\bar{x}$	s.d.	$\bar{x}$	s.d.	g wet ÷ g dry
Hypnea	580.3	295.7	84.3	52.6	5.1
Laurencia	228.5	310.9	37.4	55.2	4.5
Gracilaria	56.1	68.9	10.5	13.1	4.8
Dictyota	348.3	186.0	43.0	24.3	8.8
Digenia	37.6	60.1	9.0	15.2	4.3
Soliera	173.3	148.7	28.1	24.3	6.3
Drift algae	1128.3	611.2	176.0	102.2	....

TABLE 3

Drift algal productivity: gross and net production and respiration as estimated by a light and dark bottle oxygen technique.

SPECIES	GROSS (light-dark)	NET (light-initial)	RESPIRATION (initial-dark)	GROSS (light-dark)	NET (light-initial)	RESPIRATION (initial-dark)
	mg $O_2 \cdot (g\ dry)^{-1} \cdot hr^{-1}$			mg $C \cdot (g\ dry)^{-1} \cdot hr^{-1}$		
Hypnea	6.8	6.5	0.3	2.9	2.8	0.1
	4.1	3.8	0.3	1.8	1.6	0.1
	0.4	-1.8	2.2	0.2	-0.8	1.0
	1.4	1.3	0.1	0.6	0.6	0.0
	1.9	1.9	0.1	0.8	0.8	0.0
$\bar{x}$	2.9	2.3	0.6	1.3	1.0	0.2
s.d.	2.6	3.1	0.9	1.1	1.3	0.4
Gracilaria	3.4	3.2	0.1	1.4	1.4	0.0
	6.1	6.0	0.1	2.6	2.6	0.0
	-0.2	-2.2	2.1	-0.1	-0.1	0.0
$\bar{x}$	3.1	2.3	0.8	1.3	2.0	0.0
s.d.	3.2	4.2	1.2	1.4	0.9	0.0
Laurencia	4.2	4.1	0.1	1.8	1.8	0.0
	4.5	4.5	0.0	1.9	1.9	0.0
	0.8	0.8	0.0	0.3	0.0	0.0
	0.9	1.1	-0.2	0.4	0.5	-0.1
$\bar{x}$	2.6	2.6	0.0	1.1	1.1	0.0
s.d.	2.0	1.9	0.1	0.9	1.0	0.1
Dictyota	4.7	3.0	1.6	2.0	1.3	0.7
	0.2	-1.4	1.6	0.1	-0.6	0.7
	0.7	0.7	0.0	0.3	0.3	0.0
	10.5	10.7	-0.2	4.5	4.6	-0.1
$\bar{x}$	4.0	3.3	0.8	1.7	1.4	0.3
s.d.	4.8	5.3	1.0	2.0	2.3	0.4
Padina	0.4	0.4	0.0	0.2	0.2	0.0
	-0.6	0.6	0.0	0.3	0.3	0.0
$\bar{x}$	-0.1	0.5	0.0	0.3	0.3	0.0
s.d.	0.7	0.1	0.0	0.1	0.1	0.0

is very small compared to the mean contribution of *Thalassia* of 16.9 g $C \cdot m^{-2} \cdot day^{-1}$ (Williams 1977). The large variation associated with the rates indicated the varying states of algal health. Under the conditions of the experiments rates determined by the O_2 and ^{14}C methods were assumed to be comparable (Vollenweider 1969).

TABLE 4

Net drift algal productivity ($\bar{x} \pm$ s.d.) as estimated by O_2 and ^{14}C techniques.

SPECIES	n	mg $C \cdot (g\ dry)^{-1} \cdot hr^{-1}$ $\bar{x}$	s.d.	g $C \cdot m^{-2} \cdot day^{-1}$
Hypnea	9	1.1	1.0	1.11
Laurencia	6	1.0	0.8	0.45
Gracilaria	4	0.8	1.6	0.10
Dictyota	4	1.4	2.3	0.72
Padina	2	0.3	0.1	.....
Digenia	2	0.2	0.0	0.04
Drift algae	27	0.9	1.2	1.90

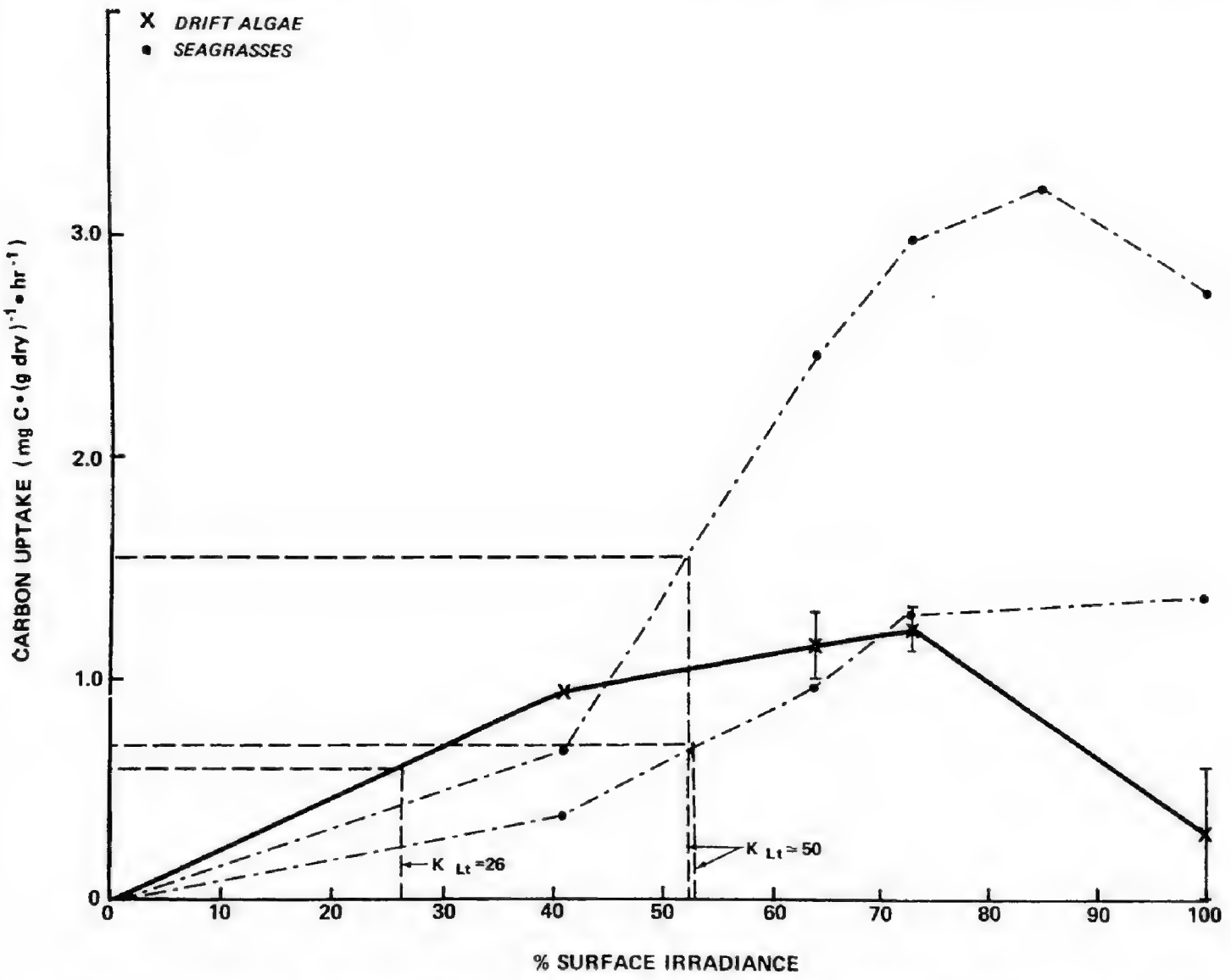

FIG 1. Productivity of drift algae; response of carbon uptake to light and competition for light among algae and seagrasses. K_{Lt} is the half-saturation constant. Seagrass data from Williams (1977).

The response of *Hypnea* productivity, as estimated by carbon uptake, to light (Figure 1) followed the typical pattern of marine production (Steeman-Neilsen 1975). Surface irradiances inhibited maximum productivity. At the half-saturation value (K_{Lt}) for light of 26% SI one half of the mean maximum rate of carbon uptake (1.22 mg C·(g dry)$^{-1}$·hr^{-1}) was achieved. This value may be used to predict productivity using the Michaelis-Menton equation and knowing surface irradiance (MacIsaac and Dugdale 1972, McRoy 1974). The alga competed for light with the seagrasses which have two basic non-competitive productive responses (Williams 1977). These responses were derived from coincident analogous experiments using the five seagrass species found in Redfish Bay. The response showing the highest maximum rate corresponded to *Halodule*, *Ruppia*, and *Halophila*. The second response corresponded to *Thalassia* and *Syringodium*. The algal response curve intersected both generalized seagrass response curves (Figure 1). The alga grew much better than the seagrasses at irradiances less than 45% SI; the algal K_{Lt} of 26% SI was about half the seagrass values of 49 to 56% SI (Williams 1977).

DISCUSSION

Most often drift algae communities are considered to increase total primary production of the system of which they become a part (Conover 1964, Pamatmat 1968). The situation may be opposite for highly productive seagrass meadows. Large accumulations of drift algae compete for and reduce light over the seagrasses which are the most important and productive plants in the system and which require much light to achieve their maximum productivity (Williams 1977). If SI is reduced 30% the seagrasses do not reach light-saturated carbon uptake and are light-limited (Figure 1). If SI is reduced 50% seagrass productivity is only half the maximum rate. In calm weather 10 to 30% SI is lost in the upper 10 cm over *Thalassia* in Texas bays (Conover 1964). A hypothetical reduction of 20% from shading by drift algae would reduce maximum rates by half in calm weather. In conditions of minimum turbidity the effect would be to prevent saturation. If 1 m^2 of *Thalassia* shaded by drift algae produces half its rate, or 8.5 g $C \cdot m^{-2} \cdot day^{-1}$, then over 4 m^2 of drift algae producing 1.9 g $C \cdot m^{-2} \cdot day^{-1}$ must exist in areas of no seagrass growth in order for drift algae to increase the total primary production of the system. The area of bare spots inhibited by drift algae is unlikely to be this extensive. The effect of shading will be more pronounced during conditions of increased wind and terrestrial run-off when up to 90% SI is attenuated in the first 10 cm over the grass beds (Conover 1964). The net productivity of drift algae may be important only in areas of poor seagrass development and in very calm weather.

The more positive contribution of drift algae to the seagrass system is provision of food, habitat and shelter for small invertebrates, especially the juvenile gastropod *Cerithidia pliculosa* and the commercial blue crab, *Callinectes sapidus*, animals which were collected often during sampling of the drift community.

Decomposition of the algae may be its most significant contribution. Decomposition will decrease oxygen concentration over the grass bed and add to the detritus system which is a major component of seagrass ecosystems (Zieman 1975).

Drift algae may also contribute to the dissolved organic carbon (DOC) pool, especially after being washed ashore and then back. From 1 to 39% of gross algal productivity may be released as DOC (Khailov and Burlakova 1969, Sieburth 1969, Brylinsky 1977). For drift algae this corresponds to 0.7 mg $C \cdot (g\ dry)^{-1} \cdot hr^{-1}$ or 1.4 g $C \cdot m^{-1} \cdot day^{-1}$.

The mobile and variable drift algae community makes contributions to the seagrass ecosystem of additional biomass, resources for animals, net production in areas of poor seagrass development, and possible influences on the detrital and chemical processes. Of most importance is its competition for and reduction of light over the highly productive seagrasses.

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LITERATURE CITED

BALLANTINE, D. and H. J. HUMM. 1975. Benthic algae of the Anclote Estuary. I. Epiphytes of seagrass leaves. *Florida Scientist.* **38**:150–162.

BARSDATE, R. J., M. NEBERT and C. P. McROY. 1974. Lagoon contributions to sediments and water of the Bering Sea. *In* D. W. Hood and E. J. Kelley (eds.), *Oceanography of the Bering Sea.* Institute of Marine Science, University of Alaska, Fairbanks. p. 553–576.

BRYLINSKY, M. 1977. Release of dissolved organic matter by marine macrophytes. *Mar. Biol.* **39**:213–220.

CONOVER, J. T. 1964. The ecology, seasonal periodicity, and distribution of bethnic plants in some Texas lagoons. *Bot. Mar.* **7**:4–41.

EDWARDS, P. 1976. *Illustrated Guide to the Seaweeds and Sea Grasses in the Vicinity of Port Aransas, Texas.* University of Texas Press, Austin.

————and D. F. KAPRAUN. 1973. Benthic marine algal ecology in the Port Aransas, Texas area. *Cont. mar. Sci.* **17**:15–52.

HUMM, H. J. 1964. Epiphytes of the seagrass, *Thalassia testudinum*, in Florida. *Bull. mar. Sci.* **14**:306–341.

ISAAC, W. E. 1956. The ecology of *Gracilaria confervoides* (L.) Grev. in South Africa with special references to its ecology in the Saldanha-Langebaan Lagoon. Proc. 2nd Itl. Seaweed Symp. p. 173–185.

KHAILOV, K. M. and Z. P. BURLAKOVA. 1969. Release of dissolved organic matter by marine seaweeds and distribution of their total organic production to inshore communities. *Limnol. Oceanogr.* **14**:521–527.

MacISSAC, J. J. and R. C. DUGDALE. 1972. Interactions of light and inorganic nitrogen in controlling nitrogen uptake in the sea. *Deep-Sea Res.* **19**:209–232.

McROY, C. P. 1974. Seagrass productivity: carbon uptake experiments in eelgrass, *Zostera marina. Aquaculture.* **4**:131–137.

MENZIES, R. J., J. S. ZANEVELD and R. M. PLATT. 1967. Transported turtle grass as a source of organic enrichment of abyssal sediments off North Carolina. *Deep-Sea Res.* **14**: 111–112.

ODUM, H. T. 1967. Biological circuits and the marine systems of Texas. *In* T. A. Olson and F. J. Burgess (eds.), *Pollution and Marine Ecology.* Interscience Publishers, New York. p. 99–157.

PAMATMAT, M. M. 1968. The ecology and metabolism of a benthic community on an intertidal sandflat. *Int. Revue ges. Hydrobiol.* **53**:211–298.

PHILLIPS, R. C. 1960. Ecology and distribution of marine algae found in Tampa Bay, Boca Ciega Bay at Tarpon Springs, Florida. *Quart. Jour. Fla. Acad. Sci.* **23**:222–255.

————. 1961. Seasonal aspect of the marine algal flora of St. Lucie Inlet and adjacent Indian River, Florida. *Quart. Jour. Fla. Acad. Sci.* **24**:135–147.

SIEBURTH, J. 1969. Studies on algal substances in the sea. III. The production of extracellular organic matter by littoral marine algae. *J. exp. mar. Biol. Ecol.* **3**:290–309.

STEEMAN-NIELSEN, E. 1975. *Marine Photosynthesis.* Elsevier, Amsterdam. 141 p.

STRICKLAND, J. D. H. and T. R. PARSONS. 1965. *A Manual of Sea Water Analysis. Bull. Fish. Res. Board of Canada.* #**125**. 203 p.

TAYLOR, W. R. 1960. *Marine Algae of the Eastern Tropical and Subtropical Coasts of the Americas.* The University of Michigan Press, Ann Arbor. 870 p.

TOPHAM, A., H. F. BITTAKER, Y. HORNELAS and J. L. ZIEGENHALS. 1975. Final report biomass-productivity group. *In* C. P. McRoy (ed.), *Biology of Seagrass Ecosystems: Report of a Summer Field Course.* Seagrass Bull. No. 1, University of Alaska, Fairbanks.

VOLLENWEIDER, R. A. 1969. *A Manual on Methods for Measuring Primary Production in Aquatic Environments.* Blackwell Scientific Publications, Oxford. 213 p.

WILLIAMS, S. L. 1977. Seagrass productivity: The effect of irradiance on carbon uptake. MS Thesis, University of Alaska, Fairbanks.

WYNNE, M. J. and W. R. TAYLOR. 1973. The status of *Agardhiella tenera* and *Agardhiella baileyi* (Rhodophyta, Gigartinales). *Hydrobiologia.* **43**:93–107.

ZIEMAN, J. C., JR. 1975. Quantative and dynamic aspects of the ecology of turtle grass, *Thalassia testudinum. Estuarine Research.* **1**:541–562.

NEW SPECIES OF AMPHIPODS FROM THE WESTERN GULF OF MEXICO[1]

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ABSTRACT

Four new species of gammaridean amphipods, *Photis macromanus*, *Parametopella texensis*, *Eripisa incisa*, and *Netamelita barnardi* are described. Keys to the unknown species of *Parametopella*, *Netamelita*, and marine *Eriopisa* are provided. Comparisons of these new species and their closest relatives lends further evidence to the importance of Pacific stock to the Atlantic amphipod fauna.

INTRODUCTION

The amphipod fauna of the western Gulf of Mexico is poorly known as there has been little systematic work in the area during recent years. An increased emphasis on obtaining ecological and distributional data on regional fauna, however, has provided a large amount of material for this type of work. Several new amphipods have been discovered among samples taken during the Texas Outer Continental Shelf Study which was supported by the Bureau of Land Management.

Four of these species described in this paper are important from both a systematic and zoogeographic standpoint. Mills (1965) has previously pointed out the close relationship of the *Ampelisca* fauna on the east and west coasts of North America and the Gulf of Mexico. The discovery of *Photis macromanus*, *Parametopella texensis*, and *Netamelita barnardi* lend further evidence of this close relationship. *N. barnardi* and another new species, *Eriopisa incisa*, are of additional importance as they provide new information on the position of their respective genera in the taxonomic hierarchy of the gammarid amphipods. The problematic relationships between *Eriopisa*, *Eriopisella*, *Melita*, and *Netamelita* have been discussed, at least in part, by a number of workers (Barnard 1970, Fox 1973, Barnard and Karaman 1975). The addition of two new species in *Eriopisa* and *Netamelita* may be of value in resolving this problem.

MATERIALS AND METHODS

Infaunal samples, from which the amphipods described in this paper were taken, were col-

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[1] University of Texas Marine Science Institute Contribution No. 256.

Table 1.

Percent sand, clay, and silt found at stations where amphipods were collected.

Species	Date	Station	Transect	Replicate No.	% Sand	% Clay	% Silt
Netamelita barnardi	Feb. 76	4	III	1	93.3	5.3	1.4
	Feb. 76	4	III	2	89.0	8.0	3.0
	Feb. 76	4	III	3	92.4	5.6	2.0
	Feb. 76	4	III	4	89.5	8.0	2.5
	Feb. 76	4	III	5	91.5	6.0	2.5
	Feb. 76	4	III	6	89.8	6.2	4.0
	Feb. 76	5	III	4	1.0	6.3	92.7
Eriopisa incisa	Feb. 76	3	I	3	8.9	65.5	25.6
	Feb. 76	6	I	5	26.6	46.5	26.9
	Feb. 76	6	II	1	1.0	68.0	31.0
	Feb. 76	6	III	1	1.0	7.0	92.0
	Mar. 76	3	II	11	4.7	65.6	29.7
	Mar. 76	6	II	1	1.2	72.6	26.2
Parametopella texensis	Feb. 76	1	I	2	34.5	44.1	21.4
	Feb. 76	4	I	5	81.2	13.2	5.6
	Feb. 76	4	III	4	89.5	8.0	2.5
	Mar. 76	SB1		4	*	*	*
	June 76	4	I	1	69.2	21.2	9.6
Photis macromanus	Feb. 76	1	I	1	57.0	26.0	17.0
	Feb. 76	1	I	3	40.0	35.0	25.0
	Feb. 76	1	I	4	35.3	44.0	20.7
	Feb. 76	1	I	5	61.0	23.4	15.6
	Feb. 76	2	I	1	21.7	44.8	33.5
	Feb. 76	1	II	1	1.0	63.0	36.0
	Feb. 76	1	II	10	*	*	*
	Feb. 76	4	III	4	89.5	8.0	2.5
	Feb. 76	4	III	6	89.8	6.2	4.0
	Feb. 76	HR1		2	*	*	*
	Apr. 76	SB3		3	*	*	*
	Apr. 76	1	II	2	55.5	29.0	15.5
	Apr. 76	1	II	4	47.6	40.4	12.0

*No sediment data

lected from the University of Texas, R/V LONGHORN, using a SMITH-MACINTYRE bottom sampler. The volume of each sample was approximately .0125 m^3 and the surface area sampled was .1088 m^2. Samples were washed through a .50 mm mesh and preserved aboard ship, then returned to the laboratory where they were sorted and identified. Sediment samples were taken from each infaunal sample and the resulting analyses for samples which contained the reported amphipods are given in Table 1.

TABLE 2

List of species, number of individuals collected, station locations and depths from February, 1976 through June, 1976.

Species	Date	Station	Transect	Replicate No.	Latitude	Longitude	Depth (Meters)	Number Individuals
Netamelita barnardi	Feb. 76	4	III	1	26°58'N	97°20'W	15	1
	Feb. 76	4	III	2	26°58'N	97°20'W	15	8
	Feb. 76	4	III	3	26°58'N	97°20'W	15	3
	Feb. 76	4	III	4	26°58'N	97°20'W	15	3
	Feb. 76	4	III	5	26°58'N	97°20'W	15	25
	Feb. 76	4	III	6	26°58'N	97°20'W	15	16
	Feb. 76	5	III	4	26°58'N	97°02'W	40	2
Eriopisa incisa	Feb. 76	3	I	3	27°34'N	96°07'W	134	3
	Feb. 76	6	I	5	27°39'N	96°12'W	100	1
	Feb. 76	6	II	1	27°24'N	96°29'W	98	1
	Feb. 76	6	III	1	26°58'N	96°30'W	125	6
	Mar. 76	3	II	11	27°18'N	96°23'W	131	1
	Mar. 76	6	II	1	27°24'N	96°29'W	98	2
Parametopella texensis	Feb. 76	1	I	2	28°12'N	96°27'W	18	1
	Feb. 76	4	I	5	28°10'N	96°29'W	10	1
	Feb. 76	4	III	4	26°58'N	97°20'W	15	2
	Mar. 76	SB1		4	26°58'N	97°20'W	79	1
	June 76	4	I	1	28°10'N	96°29'W	10	3
Photis macromanus	Feb. 76	1	I	1	28°12'N	96°27'W	18	2
	Feb. 76	1	I	3	28°12'N	96°27'W	18	1
	Feb. 76	1	I	4	28°12'N	96°27'W	18	1
	Feb. 76	1	I	5	28°12'N	96°27'W	18	2
	Feb. 76	2	I	1	27°55'N	96°20'W	42	1
	Feb. 76	1	II	1	27°40'N	96°59'W	22	2
	Feb. 76	1	II	10	27°40'N	96°59'W	22	1
	Feb. 76	4	III	4	26°58'N	97°20'W	15	2
	Feb. 76	4	III	6	26°58'N	97°20'W	15	1
	Feb. 76	HR1		2	27.53469°N	96.47203°W	74	1
	Apr. 76	SB3		3	27.43496°N	96.52962°W	85	5
	Apr. 76	1	II	2	27°40'N	96°59'W	22	2
	Apr. 76	1	II	4	27°40'N	96°59'W	22	1

Table 2 gives the station numbers, locations, and depths at which the new amphipods were collected. The numbers of individuals and collecting dates are also included. Some additional material containing specimens of *P. texensis* and *P. macromanus* from depths of 10 to 15 m near Galveston Island, Texas (Lat 94° 38′W, Long 29° 15′N) were also examined.

All types of paratype series have been deposited in the U.S. National Museum of Natural History. Other specimens have been deposited in the collection of The University of Texas Marine Science Institute, Port Aransas Marine Laboratory, Port Aransas, Texas. Additional specimens have been deposited in the working collection of the Department of Oceanography and the Invertebrate Collection of the Department of Biology at Texas A&M University, College Station, Texas.

The labeling of figures, with some modificatons, follows the style of J.L. Barnard, 1974. A capital letter designates a part and a lower case letter modifies the description of the part. All other letters are explained in the particular figure legend. B = labrum (upper lip), C = coxa, D = dactyl of peraeopod, G = labium (lower lip), H = head, J = epistome, L = palp, M = mandible, N = gnathopod, P = pepaeopod, Q = mandible molar, S = maxilliped, T = telson, U = uropod, V = urosome, W = pleon, X = maxilla, Y = prebuccal complex, Z = mandibular incisor; b = without, d = finger hinge, e = dactyl of gnathopod, f = female, h = holotype, k = cuticle, l = left, m = male, o = opposite—other side or outer, q = half of or side, r = right, s = setae removed, u = flattened, v = ventral, x = medial, y = article.

Genus **Netamelita** J. L. Barnard, 1962

Diagnosis: Uropod 3 extending beyond end of uropods 1 and 2, the inner ramus short, scale-like, accessory flagellum uniarticulate; gnathopod 2 as small as gnathopod 1, its article 6 subequal to or shorter than article 5; mandibular palp slender, articles linear; inner plates of maxilla 1 and 2 with terminal setae only.

Netamelita barnardi, new species

Figures 1–2

Description—Male 3.46 mm. Head and body normal for genus; cephalic lobes lacking, corners unproduced; ommatidia loosely organized, reduced in number; body without carina, posterodorsal edge of pleosomites 2 and 3 with short dorsal setae. Antenna 1: Length ratio of peduncular articles 1,2,3 = 19:12:5; flagellum with 13 articles poorly setose; accessory flagellum uniarticulate, half the length of the first article of flagellum. Antenna 2: 0.8 times the length of antenna one; flagellum with 6 articles. Upper lip: Epistome unproduced; labium rounded distally. Mandible: Molar triturative, dorsally setulose, molar produced; one accessory blade, reduced; right and left lacinia mobilis present; palp with 3 articles, length ratios of 9:35:25; article 3 with 3 elongate terminal setae. Lower lip: Inner lobes present; outer lobes not produced medially. Maxilla 1: Inner plate longer than wide with 2 long and 1 short terminal setae; outer plate subequal in length to the inner with 9 spine teeth; palp biarticulate, 2nd article medially expanded, terminally setose. Maxilla 2: Inner and outer plates subequal terminally setose. Maxilliped: Inner plate with terminal setae; outer plate with mediodistal spine teeth; palp with 4 articles, article 2 medially setose, article 4 with accessory spine. Gnathopod 1: Coxa produced forward; article 2 with 2 medial and 1 elongate distal setae; article 4 with group of small spines on posterior margin; article 5 with stout posterodistal setae; article 6 0.9 times

the length of article 5, margin of oblique palm lined with setae, otherwise undefined; dactyl normal. Gnathopod 2: Coxa unproduced; article 4 with spinulose posterior lobe; otherwise similar to and subequal in size to gnathopod 1. Peraeopod 3: Coxa rounded; length ratio of articles 2,4,5,6 = 22:15:9:10; posterior margin of article 6 with 2 medial spines, 2 locking spines. Peraeopod 4: Posterior margin of article 2 with 3 long setae; anterior margin of article 4 with 5 long setae; otherwise same as peraeopod 3. Peraepod 5: Article 2 expanded with longitudinal ridge; length ratio of articles 4,5,6 = 1:1:1. Peraeopod 6: Article 2 expanded, anterior margin with 5 spines and 2 groups of spines, posterior margin with row of setae; articles 4,5,6 with moderately setose margins, length ratios of 1:1:1:; overall length of peraeopod 1.5 times the length of peraeopod 5 and 1.0 times the length of 7. Peraeopod 7: Article 2 expanded with distinct posterior lobe, margin setose; margins of articles 4,5,6 moderately setose, length ratios of 15:22:18. Epimeral plates: Epimeron 1 produce slightly with 2 ventral setae; epimeron 2 also produced posteriorly, setose ventrally; epimeron 3 wider than preceding 2 with 5 ventral spines; posteroventral corner produced. Uropod 1: Peduncle with 4 outer marginal, 7 inner marginal spines and an inner and outer distal spur, basal peduncular spur also present on outer margin; rami subequal in length, each with 1 mediodorsal spine and 3–4 terminal spines. Uropod 2: Peduncle with 3 inner marginal, 1 outer marginal spines and 4 spines on inner corner; inner ramus slightly longer than outer with 2 inner marginal, 5 terminal spines; outer ramus with 2 outer marginal, 5 terminal spines. Uropod 3: Peduncle short, anterodistal corner spinulose, opposite corner with 4 spines; inner ramus 0.2 times the length of the outer, surface of article spinulose with 1 medial and 1 terminal spine; outer ramus greatly elongate, extending well beyond uropods 1 and 2, margins of ramus with 3 groups of spines, 6 terminal spines. Telson: Deeply cleft, apices rounded, with 1 spine on each lobe and 2 basal setae, 1 lateral seta, and 1 pair of medial setae. Gills: Sac-like, present on peraeopods 2–6, gill on gnathopod 2 slightly smaller than on peraeopod 3, gills 4–6 decreasing in size.

Female—Like male in general features.

Gills: Similar to those of male. Elongate linear brood plates present on gnathopod 2 and peraeopods 3–5.

Types—Holotype, (USNM #168019), male 3.46 mm. with 13 paratypes.

Type locality—Holotype and paratypes from station 4/III–6 IDF, 26° 58′N, 97° 20′W Gulf of Mexico, 15 m.

Material examined—The types plus a total of 39 specimens from the following stations: 5/III–4 IFE, 4/III–2 ICZ, 4/III–1 ICX, 4/III–4 IDD, 4/III–2 ICZ 4/III–6 IDH, 4/III–3 IDB, 4/III–5 IDF, 1/II–4 26 Feb 75.

Distribution—Gulf of Mexico, 15–40 m. depth.

Etymology—This species is named for Dr. J. L. Barnard who originally described the genus and until now its only species.

Relationships—*N. barnardi* n. sp. and *N. cortada* Barnard, 1962, are at present the only species described in this genus. *N. barnardi* differs from *N. cortada* in the following aspects: 1) coxa 1 distinctly produced into a rounded anterior lobe; 2) article 4 of gnathopod 2 with a more pronounced evntral lobe; 3) palm of

gnathopod 2 more oblique, corner less well defined than in *N. cortada*. *N. barnardi* also has an anteroproximal "spur" or spine on the peduncle of uropod 1 which is lacking in *N. cortada*. Spination of uropods 1 and 2 also differs between the two species as the outer ramus of uropod 3, in *N. cortada*, is more spinous basally than in *N. barnardi*. Rami of uropod 2 in *N. barnardi* lack inner marginal spines. Epimeral plates, gnathopod 1, peraeopods, and mouthparts of the two species are very similar and indicate a close relationship between them.

Both of these species differ from Nagata's undetermined (1960) genus and species which, as Barnard (1962b) pointed out, is undobutedly a *Netamelita*. Nagata's species differs from other netamelitids by possessing more expanded palms of the gnathopods, slender peraeopods 3–5, and pointed apices of telsonic lobes.

Ecological information—Salinity range: 35.09–36.06 ‰ temperature range: 15.29–20.29°C; sediment preference: sand. Although both species of this genus were collected from a similar range of depths, *E. cortada* was found on rock bottoms.

Key to the known species of **Netamelita***

1. Lobes of telson pointed, palm of gnathopod 1 twice as long as hind margin of article 6 ..... Nagata's sp.
1. Lobes of telson rounded, palm of gnathopod 1 less than 1.5 times as long as hind margin of article 6 2
2. Peraeopods 3–5 with lateral accessory nails, coxa 1 unproduced ..... **N. cortada**
2. Peraeopods 3–5 lacking lateral accessory nails, coxa 1 produced anteriorly ..... **N. barnardi**

* Including Nagata's unnamed species.

Genus **Eriopsia** Stebbing, 1890

Diagnosis: Uropod 3 extending beyond end of uropods 1 and 2, inner ramus short, scale-like, outer ramus biarticulate with second article subequal to or shorter than first; accessory flagellum biarticulate; inner plates of maxilla 1 and 2 with dense medial seate.

Eriopisa incisa, new species

Figures 3–5

Description—Male 4.27 mm. Head without eyes, inferior antennal sinus deeply incised; body otherwise normal for genus. Antenna 1: Article 1 of peduncle with medioventral group of setae, 1 distoventral spine; article 2 of peduncle 1.1 times as long as article 1; third article 0.3 times length of article 2; flagellum with 18–22 articles; accessory flagellum with 2 articles. Antenna 2: Article 4 of peduncle 1.1 times length of article 5, both linear, poorly setose; flagellum with 7

articles. Upper lip: Distally rounded, somewhat produced medially. Mandible: Molar produced, rounded, triturative, surface setulose with setule row and accessory setae; incisor with 5 rounded teeth, well produced; lacinia mobilis with 2 bifid lobes present on both right and left mandibles; 8 accessory blades on either mandible; palp with 3 articles of length ratio 21:73:127; article 3 with group of elongate terminal setae; articles otherwise poorly setose. Lower lip: Outer lobes widely separated; inner lobes present. Maxilla 1: Inner plate medially setose; outer plate with terminal spine-teeth; palp biarticulate, distal article 4.0 times as long as article 1; article 2 with 8 short terminal setae. Maxilla 2: Plates subequal in length; outer with terminal setae; inner with medial setae and one row of diagonal facial setae. Maxilliped: Inner plate terminally truncate with chisel spines; outer plate also truncate terminally, lacking chisel spines; palp with four articles, article 3 distally setulose, article 4 medially setulose. Gnathopod 1: Much smaller than gnathopod 2; article 4 with distomedial setae, ventrally setulose; 5th article 1.1 times the length of article 6, with 3 rows of mediofacial and 1 row of ventral setae; palm oblique, straight, distally expanded and lined with short spines, palmar corner defined by group of small spines, hind margin straight; dactyl tapering, closing on corner. Gnathopod 2: Coxa quadrate, wider than long; article 2 with 7 setae on posterior margin; article 5 with ventral setae, 0.5 times the length of article 6; palm poorly distinguished from hind margin but defined by 2 stout spines, palm lined with short spines, 1 stout medial spine; dactyl elongate, tapering. Peraeopod 3: Articles linear, length ratio of articles 4,5,6 = 16:17:13; posterior margin of article 6 with setal formula of 1,2,2,2,2,2. Peraeopod 4: same as 3. Peraeopod 5: article 2 more expanded than preceding ones, anterior margin with 5 spines, posterior margin proximally serrate, length ratio of articles 4,5,6 = 17:12:12. Peraeopod 6: article 2 expanded, anterior margin with 9 spines, posterior margin serrate along 2/3 of proximal margin; length ratio of articles 4,5,6 = 43:38:36; posterior margin or article 6 with 2 medial setae. Peraeopod 7: article 2 expanded, anterior margin with 11 spines, posterior margin serrate; length ratio of articles 4,5,6 = 20:18:19; anterior margin of article 6 with setal formula of 2,2,2; peraeopod 1.1 times the length of 6. Epimeral plates: Epimeron 2 with 5 elongate, plumose setae; epimeron 3 posterior corner produced, ventral edge with 3 spines. Uropod 1: Inner and outer margin of peduncle lined with spines; inner and outer distolateral corners and laterobasal margin with 1 "spur" type spine each; inner ramus with 5 inner, 1 outer marginal spines and 3 terminal spines; outer ramus with 2 inner marginal, 2 outer marginal spines and 4 terminal spines. Uropod 2: Inner margin of peduncle with 2 marginal spines and distal cluster of 3 spines; outer margin with 3 spines and distal cluster of 2 spines; inner ramus with 4 inner marginal, 2 outer marginal spines and 5 terminal spines; outer ramus with 2 spines on both inner and outer margins and 5 terminal spines. Uropod 3: Outer ramus with 2 articles, second article 0.7 times the length of the first; 1st article with 1 medial spine, 5 terminal spines; article 2 with 4 scattered spines and one group of terminal setae; inner ramus reduced, scale-like with 2 terminal, 1 medial spine. Telson:

Deeply cleft, apices pointed, distolateral corner of each lobe with 1 spine and row of 3 setae. Gills: Sac-like, present on gnathopod 2 and peraeopods 3–6, gills 5 and especially 6 reduced.

Female—4.27 mm. The female differs from male only in having more setose peraeopods. Gnathopods and head are similar to that of male, uropod 3, however, is unknown for the female. Elongate, linear brood plates are present on gnathopod 2 and peraeopods 3–5. Juveniles differ from adults in that the palm of gnathopod 2 lacks spines, palmar corner is defined by cluster of 3 elongate setae. Incised corner of head is less well developed in juvenile but obvious. Juvenile is otherwise like female.

Types—Holotype, (USNM #168014), male 4.67 mm. with 1 allotype, (USNM #168017), female 4.27 mm. and 7 paratypes.

Type locality—Holotype from station 5/II–1 HOZ, Gulf of Mexico, 27° 24′N–96° 29′W, 98 m. Allotype from station 6/III–1 IGH, Gulf of Mexico, 26° 28′N–96° 30′W, 125 m.

Material examined—The types and specimens (a paratype series) from the following stations: 2 males and 1 female–3/I–3 HDJ, 2 juveniles and 2 males–6/III–1 IGH, 1 male–6/I–5 HGX.

Distribution—Gulf of Mexico, 98–134 m depth.

Etymology—The specific name refers to the deeply incised inferior antennal sinus.

Relationships—E. incisa n. sp. shows close relationship to *E. elongata* (Bruzelius) 1859, a North Atlantic species. Both species agree in a number of features which distinguish them from other members of the genus. The inferior antennal sinus of both species is incised; the dorsal lobe of *E. incisa*, however, is produced to a point while that of *E. elongata* is rounded. The mandibular palps of both species are similar in the linear structure of the third article and in having the third article longer than the second. The outer rami of uropod 3 are also similar in structure and relative lengths of their two articles. The anteriorly produced first coxa, structure and armament of the gnathopods and telson, and the structure of epimeron 3 serve as further evidence of the close relationship between these two species.

The other species, *E. epistomata*, Griffiths, 1974 from the southwestern coast of Africa, and *E. garthi*, J. L. Barnard, 1952 from the lower California coast of Mexico also appear to be closely related to *E. incisa*, although not to be the same degree as *E. elongata*. *Coxa* 1, structure of gnathopods, telson, epimeron 3, and uropod 3 are all similar to those of *E. incisa* and *E. elongata*.

E. epistomata differs from the aforementioned species primarily in having a slightly concave palm on gnathopod 2, as compared to a straight palm in *E. incisa* and *E. elongata*. Article 3 of the mandibular palp is also medially expanded in *E. epistomata*. The structure of uropod 3 and the produced corner of epimeron 3 in *E. garthi* resemble those species mentioned above. Article 3 of the mandibular palp, however, is closer to that of *E. epistomata* than the other two and there is a definite sinus in the palm of gnathopod 2. *E. garthi* differs from *E. incisa*, *E. epis-*

tomata and *E. elongata* in having rounded telsonic apices, nontriangulate article 6 of gnathopod 1, and a rectangular first coxa.

J. L. Barnard (1976) redefined a number of families and genera of gammaridean amphipods including the genus *Eriopisa*. In this paper Barnard removed *Eriopisa longiramus* Stock and Nijssen, 1965 and *E. caeca* (S. Karaman) 1955 to the revived genus *Psammogammarus*. Zimmerman and Barnard (1977) further restricted the *Eriopisa* by transferring *E.* (?) *hamakua* J. L. Barnard, 1970 to *Dulzura* and *E. laakona* J. L. Barnard, 1970 to *Hadzia*. The marine species of *Eriopisa* are therefore restricted to: *E. elongata* (Bruzelius) 1859; *E. epistomata* Griffiths, 1974; *E. garthi* J. L. Barnard, 1952; and *E. incisa*, n. sp.

Ecological information—Salinity range: 36.25–36.56 ‰; Temperature range: 17.59–19.86° C; sediment preference: high percentage of clay. *E. incisa* differs from *E. garthi* in habitat preference as the latter was initially collected from under intertidal rocks. *E. epistomata*, like *E. incisa*, was found in bottom mud but at depths of only 6–11 m.

Key to the Marine Species of the Genus **Eriopisa***

1. Anteroventral corner of head not incised; article 3 of mandibular palp linear, longer than article 2 2
1. Anteroventral corner of head not incised; article 3 of mandibular palp expanded medially or not, shorter than article 2 3
2. Dorsal and ventral lobe of incised inferior antennal sinus produced to a point, subequal in length; margins of both articles of inner ramus on uropod 3 poorly spinose ..... **E. incisa**, n. sp.
2. Dorsal lobe of inferior antennal sinus rounded, longer than ventral lobe; margins of both articles of inner ramus on uropod 3 lines with spines ..... **E. elongata** (Bruzelius) 1859
3. Coxa 1 produced to an anterior point; apices of telson pointed; palm of gnathopod 2 with shallow sinus ..... **E. epistomata** Griffiths, 1974
3. Coxa 1 rectangular; apices of telson rounded; palm of gnathopod 2 with deep sinus ..... **E. garthi** J. L. Barnard, 1952

* A key to other species of the genus may be found in Stock and Nijssen, 1965.

Genus **Parametopella** Gurjanova, 1938

Diagnosis: Mandible without palp; maxilla 1 with uniarticulate palp; article 2 of peraeopods 3–5 linear, not expanded.

Parametopella texensis, new species

Figures 5–7

Description—Female 3.35 mm. Head normal for genus; eyes round, well developed; segments 2 and 3 of urosome fused. Antenna 1: Article 1 of peduncle not produced anterodistally; length ratio of peduncular articles = 45:43:14; flagellum with 19 articles; accessory flagellum lacking. Antenna 2: 1.2 times the

length of antenna 1; article 5 of peduncle 1.2 times the length of article 4; flagellum with 6 articles. Upper lip: Wider than long, bilobed. Mandible: Molar process vestigil, represented by raised lobe with 1 spine on left mandible, spine missing on right; 8 accessory blades on the left and 9 on the right mandible; incisor broad with 9 teeth and 1 stout spine on lower corner; left lacinia mobilis present, right absent; area between incisor and accessory blades of irght mandible with several broadly flattened to broadly rounded setae, tops serrate; left mandible with two similar, but "barrel" shaped setae below lacinia mobilis; palp lacking. Lower lip: Outer lobes widely separated; inner lobes apparently fused and of unusual orientation, this lobe "anvil-shaped," its long axis perpendicular to that of outer lobes in linguiform manner projecting inward toward mandibles. Maxilla 1: Inner plate reduced, unarmed; outer plate with 6 spine teeth; palp uniarticulate with 5 medial, 2 terminal spines. Maxilla 2: Inner plate reduced, with 6 mediodistal setae; outer plate longer than inner, with 7 terminal setae. Maxilliped: Inner plates fused together, reduced, poorly setose; outer plates obsolescent; palp with 4 articles, well developed, medially spinous; articles 3 and 4 distally setulose. Gnathopod 1: Coxa quadrate, reduced, hidden by coxa 2; anterior edge of article 2 lined with setae; article 4 with ventral lobe; setulose, with 6 elongate spines; elongate article 5 with 5 elongate mediofacial spines, spiculate ventral margin with 8 spines; article 6 spiculate along length of palm, otherwise poorly distinguished from hind margin; sixth article 0.7 times as long as article 5. Gnathopod 2: Coxa large, produced anteriorly, broadly rounded with 3 ventral spines; article 2 elongate, anterior margin spinose; article 5 with spinose ventral lobe; article 6 expanded distally, palm oblique, lower corner defined by spinose tooth; finger hinge process with 5 lobe complex; anterior edge of article 6 with widely spaced, blunt spicules, gnathopod 2 much larger than 1. Peraeopod 3: Coxa of slightly less area than coxa 2, posteroventral margin with 10 spines, plate produced forward slightly; anterior margin of article 2 spinose; articles 4–6 without spines, length ratios of articles 4,5,6 = 43:32:57. Peraeopod 4: Coxa of immense area, covering posterior half of coxa 3, all of coxal plates 5–7, epimeral plate 1 and proximal articles of peraeopods 5–7; length ratio of articles 2,4,5,6 = 100:52:35:58. Peraeopod 5: Coxa wider than long with sharply produced posterior lobe; length ratios of articles 2,4,5,6 = 88:43:33:42; total length 0.8 times as long as peraeopod 4; remaining peraeopods of successively decreasing lengths. Peraeopod 6: Coxa with slightly produced posterior lobe; articles poorly spinose, length ratios of articles 2,4,5,6 = 78:39:34:47. Peraeopod 7: Coxa wider than long; poorly spinose, length ratios of articles 2,4,5,6 = 59:30:29:49; total length 0.8 times that of peraeopod 6. Epimeral plates: Empimeron 1 wide as long; remaining plates unproduced, unarmed. Uropod 1: Peduncle elongate; inner margin bare except for 1 distal spine; outer margin with 6 spines; rami subequal in length, lanceolate; inner ramus with 1 inner marginal spine; outer ramus with 2 outer marginal spines; margins of peduncle and rami minutely serrate. Uropod 2: Inner margin of peduncle without spines, outer margin with 3 spines, mediodistal edge with 1 spine, margins of peduncle minuately serrate; rami lanceolate, unarmed, margins minutely serrate. Uropod 3: Uniramus, peduncle 0.6 times the

length of biarticulate, lanceolate ramus; second article of ramus 1.4 times the length of the first. Telson: Entire, longer than wide, apex rounded.

Male—Unknown for this species.

Types—Holotype, (USNM #168026), female 3.35 mm. with 2 paratypes.

Type locality—Holotype from station 4/III–4 IDD, Gulf of Mexico, 26° 58′N–97° 20′W, 15 m.

Material examined—The type specimen, 1 female from the type locality, and 1 female from station 1/I–2 HAC–1. Six specimens from the waters off Galveston Island, Texas were also examined.

Distribution—Gulf of Mexico, 10–18 m. depth.

Etymology—Specific name refers to type locality on the Texas coastal shelf.

Relationships: *P. texensis* appears to be an intermediate between *P. ninis* J. L. Barnard, 1962c from the California coast, and *P. inquilinus* Watling, 1976 from Delaware Bay, U.S.A. although it is more similar to the latter. *P. texensis* differs from *P. inquilinus* in the following: 1) flagellum article 1 of antenna 1 subequal to others in *P. texensis* whereas twice the length of remaining articles in *P. inquilinus*, 2) inferior antennal sinus more excavate in *P. texensis*, 3) article 3 of maxilliped longer in *P. texensis*, 4) coxa 1 longer than wide in *P. texensis* and wider than long in *P. inquilinus*, 5) posterior edge of coxa 3 spinose in *P. texensis*, not so in *P. inquilinus*, 6) anterior edge of peraeopod 3 lined with spines in *P. texensis* whereas *P. inquilinus* has only proximal spines, 7) posterior edge of coxa 5 produced in *P. texensis*, not so in *P. inquilinus*, 8) epimeral plate 1 of *P. texensis* rounded, unlike that of *P. inquilinus*.

Another closely related east coast species is *P. cypris* (Holmes) 1905 which shares some similarities with the three species previously mentioned. Coxal plates 2 and 3 of *P. texensis* are somewhat similar to those of *P. cypris*; however, the lower margins of the plates in *P. texensis* and *P. inquilinus* are free as they are in *P. ninis*. Peduncular areas 4 and 5 of antenna 2 in *P. texensis*, *P. inquilinus* and *P. ninis* are longer than the relatively shorter articles in *P. cypris*. The length of the article 5, gnathopod 2 in *P. texensis* is intermediate between *P. ninis* and *P. cypris*, although the ventral lobe of *P. texensis* is closer to that of *P. cypris*. *P. cypris*, *P. inquilinus* and *P. texensis* differ from *P. ninis* in having their telsons and ramus of third uropods unarmed, and epimeral plates unproduced. Urosomites 2 and 3 of *P. ninis*, *P. inquilinus* and *P. texensis* are apparently fused while separate in *P. cypris*. *P. texensis* differs from both *P. ninis* and *P. cypris* in that the anterior margins of article 2 of the gnathopods are more spinose.

All four of the above species differ from *P. stelleri* Gurjanova, 1948 by lacking the anterodistal process of peduncular article 1 of antenna 1 and by bearing more elongate ramus on uropod 3. Both gnathopods in *P. stelleri* are of greatly different structure than in other members of the genus.

Ecological information—Salinity range: 30.15–36.56 ‰; temperature range: 15.23–27.12° C; sediment preference: sand. Other members of this species, *P. cypris* for example, are commonly found on hydroids, ectoprocts and sponges immediately subtidal to deeper channels (Bousfield 1973). No such information is available on *P. texensis* but its distribution does resemble that of the California

species, *P. ninis*, which is restricted to coastal shelfs of 10–30 m depth (Barnard 1962c). None of the parametopellids are common (*P. ninis* 0.5 animals per sq. m.) and males of the genus are poorly known. Watling (1976) reports males of *P. inquilinus* as smaller but similar to the females.

Key to the species of the genus **Parametopella**

1. Article 1 of antenna 1 with anterodistal process ..... **P. stelleri** Gurjanova, 1948
1. Article 1 of antenna 1 lacking anterodistal process 2
2. Lateral edges of telson armed with spines ..... **P. ninis** J. L. Barnard, 1962
2. Lateral edges of telson unarmed 3
3. Inferior antennal sinus poorly excavate, coxa 1 wider than long, poterior edge of coxa 3 unarmed ..... **P. inquilinus** Watling, 1976
3. Inferior antenna sinus excavate, coxa 1 longer than wider, posterior edge of coxa 3 armed 4
4. Articles 4 and 5 of antenna 2 elongate, subequal; gnathopod 2 with medial palmar process ..... **P. texensis** n. sp.
4. Article 5 of antenna 2 shorter than 4; gnathopod 2 without medial palmar process ..... **P. cypris** (Holmes), 1905

Genus **Photis** Krøyer, 1842

Diagnosis: Accessory flagellum absent or represented by vestigal scale; article 3 or antenna 1 equal to or longer than article 1; uropod 3 biramus, inner ramus much shorter than outer.

Photis macromanus, new species

Figures 7–10

Description—Male 2.19 mm. Head normal for genus, eyes well developed, darkly pigmented; cephalic lobe sharply rounded. Antenna 1: Article 2 of peduncle longest, length ratios of peduncular articles = 83:117:85; flagellum with 5 articles, each article with distal, elongate, flattened setae, apical article with 2 such setae; accessory flagellum rudimentary. Antenna 2: Article 4 of peduncle 1.2 times the length of article 5; flagellum with 4 articles. Upperlip: Epistome somewhat produced; labrum weakly bilobed. Mandible: Molar triturative, produced, right molar with rugose accessory lobe, left molar with accessory setae only; 4 accessory blades on left and 3 on right; lacinia mobilis present on both mandibles; incisor with 5 rounded teeth; palp with 3 articles, length ratios of 25: 72:55, ventral margin of article 2 setose, article 3 distoventrally setose, palp stout, well developed. Lower lip: Inner lobes present; outer lobes apically rounded, well developed. Maxilla 1: Inner plate rounded, reduced and unarmed; outer plate with 9 spine teeth; palp biarticulate, second article 5 times length of first, with 6 terminal spines and oblique row of mediofacial spines. Maxilla 2: Inner plate of less area than outer, with mediodistal setae and oblique row of basomedial facial setae. Maxilliped: Inner plate short, apically truncate with 3 chisel spines and oblique row of distomedial setae; outer plate with 5 chisel spines and double row

of mediofacial setae along inner margin; palp with 4 articles, medially setose, article 3 apically setose, article 4 with accessory spine. Gnathopod 1: Coxa longer than wide, ventral margin with 10 setae; article 4 with distoventral setae; article 5 with poorly developed, setose ventral lobe; palm slightly concave, lower corner defined by tooth with 1 large spine, palm poorly setose; dactyl with small mediodistal spine. Gnathopod 2: Coxa as long as first coxa but slightly wider with 7 ventral setae; lateral surface of article 2 with oblique row of stridulating ridges, anterior margin with 3 elongate plumose setae, ventral margin with 2 elongate setae; article 5 with unarmed ventral lobe; article 6 well developed; poorly seose; palm with deep, sharply excavate sinus; lower corner defined by elongate, sharply produced, setose tooth; dactyl flattened, inner margin somewhat serrate with 4 distomedial spines, dactyl overlapping defining tooth of palm. Peraeopod 3: Coxa quadrate, length subequal to preceding coxa, ventral margin with a row of stridulating ridges and 5 ventral setae; article 2 with 2 elongate spines on anterior margin, ventral margin with 2 proximal spines, 2 elongate medial setae, and 3 distal plumose setae; article 4 with setose anterior lobe; length ratios of articles 4,5,6 = 43:26:55; articles 2, 3 and 4 glandular. Peraeopod 4: Coxa similar to coxa 3 but without stridulations, and with 3 ventral setae; article 4 with 4 anterior and 3 posteromarginal finely pulmose setae; anteriodistal corner of article 5 with long finely plumose setae; otherwise like peraeopod 3. Peraeopod 5: Coxa 5 slightly larger than 4 with well developed posterior lobe; article 2 greatly expanded with dorsoventral ridge down medial surface, anterior edge with 4 plumose setae; length ratio of articles 4,5,6 = 29:30:40; article 6 with 2 distal locking spines; dactyl with accessory claw. Peraeopod 6: Coxa small, wider than long; article 2 expanded, with 3 posteromarginal spines and 5 plumose anteromarginal setae; remaining articles linear, poorly spinose; length ratios of articles 4,5,6 = 21:20:30, article 6 with 2 locking spines; 1.35 times the length of peraeopod 5. Peraeopod 7: Coxa longer than wide, produced posteriorly; article 2 expanded with 1 posteromarginal and 5 anteromarginal plumose setae; otherwise same as peraeopod 6. Epimeral plates; Rounded, unproduced, epimeron 3 with 1 small medioventral spine. Uropod 1: Inner margin of peduncle with 1 distal spine, outer margin with 5 spines; rami subequal in length; inner margin of inner ramus with 1 medial and 1 terminal spine; outer margin of outer ramus with 2–4 spines and 1 terminal spine. Uropod 2: Inner margin of peduncle with 1 distal spine, outer margin with 2 spines; outer ramus 0.75 times the length of inner; inner margin of inner ramus with 2 medial and 2 terminal spines; outer ramus with 1 mediodistal and 2 terminal spines. Uropod 3: Peduncle longer than rami, unarmed; inner ramus short, 0.2 times length of outer ramus, with 1 terminal spine; outer ramus biarticulate, article 1 with 1 mediodistal spine, article 2 minute, with 3 terminal setae, 2 of these flattened and "blade-like" one of which twice as long as the other. Telson: Long as wide, triangulate, dorsally forming open "cup" containing 2 pair of setae and 1 pair of setules.

Female—2.97 mm. The female differs from the male chiefly in the structure of gnathopods. The ventral margin of article 5 of gnathopod 1 is longer and more setose in the female. The palm of gnathopod 1 lacks a defining tooth but is other-

wise similar to that of the male. Gnathopod 2 of the female is much smaller than that of the male, yet longer than its respective first gnathopod. The ventral lobe of article 5 on gnathopod 2 is more pronounced in the female than in the male and the large defining tooth and deep sinus of the male's second gnathopod are absent. The female's palmar corner is defined by a small tooth and 1 spine and article 6 is somewhat oval in shape in contrast to the more elongate sixth article of the male. The stridulating ridges on the second article of gnathopod 2 and the ventral margin of coxa 3 of the male are absent on the female.

Type—Holotype, (USNM #168021), male 2.19 mm. with 1 allotype, (USNM #168022), female 2.97 mm. and 5 paratypes.

Type locality—Holotype from station 1/I HAA, Gulf of Mexico, 28° 12′N–96° 27′W, 18 m. Allotype from the same station as the male.

Material examined—The types and specimens (a paratype series) from the following stations: 2 females–4/III–6 IDH, 2 females–1/I–5 HAI, 1 female–2/I–1 HBW. Other specimens from waters near Galveston Island, Texas were also examined.

Distribution—Gulf of Mexico, 18–42 m. depth.

Etymology—Specific name refers to the well developed gnathopod 2 of the male.

Relat onships—*P. macromanus* has its closest relationship to *P. conchicola* Alderman, 1936 based on the structure of gnathopod 2, stridulating structures, and peracopods. Both species have a deep conical sinus and long projecting tooth on the palm of gnathopod 2. The form of the dactyl and finger hinge process are also similar in both species. Although coxa 1 of *P. macromanus* is more elongate and narrower than in *P. conchicola*, coxa 3 is quite similar in both species. The lobate articles and accessory claw of peraepod 5 and the structure of peraeopods 6 and 7 are also similar in both species. The peraeopods of *P. macromanus*, however, appear to be less spinose. The two species differ in that *P. conchicola* lacks the palmar defining tooth of gnathopod 1 which is found in *P. macromanus*. They also differ in armanent of uropods as *P. conchicola* is more spinose.

Female gnathopods also differ in structure and armanent. The palm of gnathopod 1 in *P. marcromanus* is much better defined although similarly armed. Gnathopod 2 of *P. conchicola* is much stouter than in *P. macromanus* but the coxal plate is less quadrate and shorter. The palm of gnathopod 2 in *P. conchicola* is more oblique and less well defined than in *P. macromanus*.

P. macromanus also appears to be a smaller species than *P. conchicola*. J. L. Barnard (1962a) shows a male *P. conchicola* of 3.7 mm. length with a well developed gnathopod 2. In the same paper he shows what is described as a young male of 2.0 mm. length with a gnathopod 2 more similar to that of a female. A male of *P. macromanus*, 2.19 mm. in length, described in this paper has a well developed second gnathopod similar to that of the adult *P. conchicola*. Egg-bearing females in the size range of the male *P. macromanus* have also been found.

Ecological information—Salinity range: 33.00–36.20 ‰; temperature range: 15.33–20.48° C. Sediment preference: bottoms with a high percentage of sand.

Unlike *P. conchicola*, a common rocky intertidal species, *P. macromanus* appears to be restricted to subtidal sandy bottoms.

ZOOGEOGRAPHY

Three of the new species described in this paper, *P. texensis*, *N. barnardi*, and *P. macromanus* are of particular zoogeographic interest as they suggest an interconnection between the Gulf of Mexico-Caribbean area and Pacific amphipod faunas. Morphological comparisons between the species described in this paper and other members of their respective genera indicate that the east coast forms may have been derived from Pacific stock.

Strongly spinose or setose peraeopods, uropods and telsons can be considered the plesiomorphic condition among amphipods and conversely a decrease in the number of spines and setae can be considered the apomorphic state. In comparing *Parametopella ninis* (Pacific coast) and the two most closely related east coast species, *P texensis* and *P. inquilinus*, it appears that the latter two are the derived forms. This consideration is based on the presence of unarmed telsons and poorly armed uropods of the east coast species. *Netamelita barnardi* (Gulf of Mexico) also demonstrates a more apomorphic condition than does *N. cortada* (California coast). The more poorly spinose condition of the uropods in *N. barnardi* has been mentioned previously and would indicate that the Gulf species could be derived from the Pacific form.

In contrast to the aforementioned species *Photis macromanus* is a member of a large and widely distributed genus. Within the photids, however, *P. macromanus* shows a close morphological affinity to *P. conchicola*, a west coast species. The apparent similarities, which were previously mentioned in the description of the new species, lend support to the close relationships of Atlantic and Pacific photids.

The relationships of *E. incisa* and other members of this genus are not as clear as in the other newly described species. *E. incisa* is quite close to *E. elongata*, a North Atlantic species and in a lesser degree to *E. epistomata* and *E. garthi*. *E. epistomata* was described from the southwestern coast of Africa and *E. garthi* from the Baja California coast of Mexico. *E. incisa* however, may also represent an intermediate species between the east and west coasts as preliminary examination seems to suggest.

In the earlier studies both J. L. Barnard (1960) and Mills (1965) have suggested that at least some amphipods spread from the eastern Pacific into the Atlantic by crossing Central America previous to the emergence of a complete land bridge during the Pliocene. Barnard (1960) noted that of the 23 species of the genus *Paraphoxus* (fam: Phoxocephalidae) that occurred in the North Pacific, 4 also occurred in the North Atlantic. Mills (1965) provided further evidence in his zoogeographic analysis of the genus *Ampelisca* (fam: Ampeliscidae). Based on morphological similarities, he separated the Northern hemisphere ampeliscids into two major species flocks consisting of an eastern North Pacific and West

African component. In further analysis Mills concluded that the eastern North Pacific fauna was more closely related to the western Atlantic (including the Gulf of Mexico and Caribbean Sea) fauna than to that of West Africa.

The present distribution of a large number of amphipods on the east and west coasts of North America could be explained by the presence of a Central American seaway in the past. The Gulf of Mexico and Caribbean Sea appear to serve as a region in which "intermediate" species have become established. Previous studies, the discovery of the species described in this paper, and studies presently underway tend to support this idea.

ACKNOWLEDGMENTS

We wish to acknowledge the U.S. Bureau of Land Management for the financial support of the South Texas Outer Continental Shelf Monitoring Study, contract number AASSO-CT6-17. We also wish to thank Dr. Don Harper for providing specimens and Dr. E. L. Bousfield for reviewing the manuscript of this paper.

LITERATURE CITED

ALDERMAN, A. L. 1936. Some new and little known amphipods of California. *Univ. Calif. Publs Zool.* **41**(7):53–74, 51 figs.

BARNARD, J.L. 1952. A new species of amphipod from Lower California (Genus *Eriopisa*). *Pacific Sci.* **6**(4):295–299, figs. 1–2.

————. 1960. The amphipod family Phoxocephalidae in the eastern Pacific Ocean, with analysis of other species and notes for the revision of the family. *Allan Hancock Pac. Exped.* **18**(3):1–375, 75 plates.

————. 1962a. Benthic marine Amphipoda of southern California: Families Aoridae, Photidae, Ischyroceridae, Corophiidae, Podocaridae. *Pacific Nat.* **3**(1):1–72, figs. 1–32.

————. 1962b. Benthic marine Amphipoda of southern California: Families Tiroidae to Gammaridae. *Pacific Nat.* **3**(2):73–115, figs. 1–23.

————. 1962c. Benthic marine Amphipoda of southern California: Families Amphilochidae, Leucothoidae, Stenothoidae, Argissidae, Hyalidae. *Pacific Nat.* **3**(3): 116–163, figs. 1–23.

————. 1970. Sublittoral Gammaridean (Amphipoda) of the Hawaiian Islands. *Smithsonian Contr. Zool.* **34**:1–286, figs. 1–180.

————. 1974. Gammaridean Amphipoda of Australia, Part II. *Smithsonian Contr. Zool.* **139**:1–148, figs. 1–83.

————. 1976. Affinities of *Paraniphargus lelouparium* Monod, a blind anchialine amphipod from the Galapagos Islands. *Proc. Biol. Soc. Wash.* **89**(36):421–432.

———— and G. S. Karaman. 1975. The higher classification in amphipods. *Crustaceana* **23**(3):304–310.

BARNARD, K. H. 1916. Contributions to the crustacean fauna of South Africa. 5. The Amphipoda. *Ann. So. African Mus.* **15**(3):105–302, pls. 26–28.

BOUSFIELD, E. L. 1973. *Shallow-water Gammaridean Amphipoda of New England.* Cornell University Press, Ithaca, N.Y. 312 p. 69 plates, 13 figs.

BRUZELIUS, R. M. 1859. Bidrag till Kannedomen on Skandinaviens Amphipods Gamaridea. *K. Svenska Vetensk Akad. Handl.* **3**(1):1–104.

FOX, R. S. 1973. *Ceradocus shoemakeri* and *Eriopisa schoenerae*, new amphipods (Crustacea: Gammaridae) from the Bahama Islands. *J. Elisha Mitchell Scient. Soc.* **89**(1/2): 147–159, figs. 1–8.

GRIFFITHS, C. L. 1974. The Amphipods of southern Africa. 2. The Gammaridea and Caprellidea of South West Africa of 20°S. *Ann. So. African Mus.* **62**(6):169–208, figs. 1–7.

GURJANOVA, E. 1948. Amphipoda Tixogo Akeana II. Stenothoidae del' nevostochnyx moric. Notebooks of the Academician Sergei Alekseyich Zernov (Hydrobiologist). pp. 287–325 and 21 figs.

HOLMES, S. J. 1905. The Amphipods of Southern New England. *Bull. Bur. Fisheries, Wash.* **24**:459–529, 13 pls. + figs.

KARAMAN, S. 1955. Ueber einige Amphipoden des Gryundwassers der jugoslavischen Meeresküste. *Acta Mus. Maced. Sci. Nat.* **2**(11–22):223–241.

MILLS, E. L. 1965. The zoogeography of North Atlantic and North Pacific Ampeliscid amphipod crustaceans. *Syst. Zool.* **14**(2):119–130, 1 fig.

NAGATA, K. 1960. Preliminary notes on benthic gammaridean Amphipoda from the *Zostera* region of Mihara Bay, Seto Inland Sea, Japan. *Publs Seto. mar. biol. Lab.* **8**(1):163–182, 2 figs., pls. 13–17.

STOCK, J. H. and H. H. NIJSSEN. 1965. *Eriopisa longiramus* n. sp., a new subterranean amphipod from a Red Sea island. *Bull. Sea. Fish. Res. Sta. Israel.* **38**:28–39, figs. 1–8.

WATLING, L. 1976. *Parametopella inquilinus*, new species from Delaware Bay oyster beds. *Proc. Biol. Soc. Wash.* **88**(39):429–432.

ZIMMERMAN, R.J. and J. L. BARNARD. 1977. A new genus of primitive marine hadziid from Bimini and Puerto Rico. *Proc. Biol. Soc. Wash.* **89**(50): 565–580, figs. 1–5.

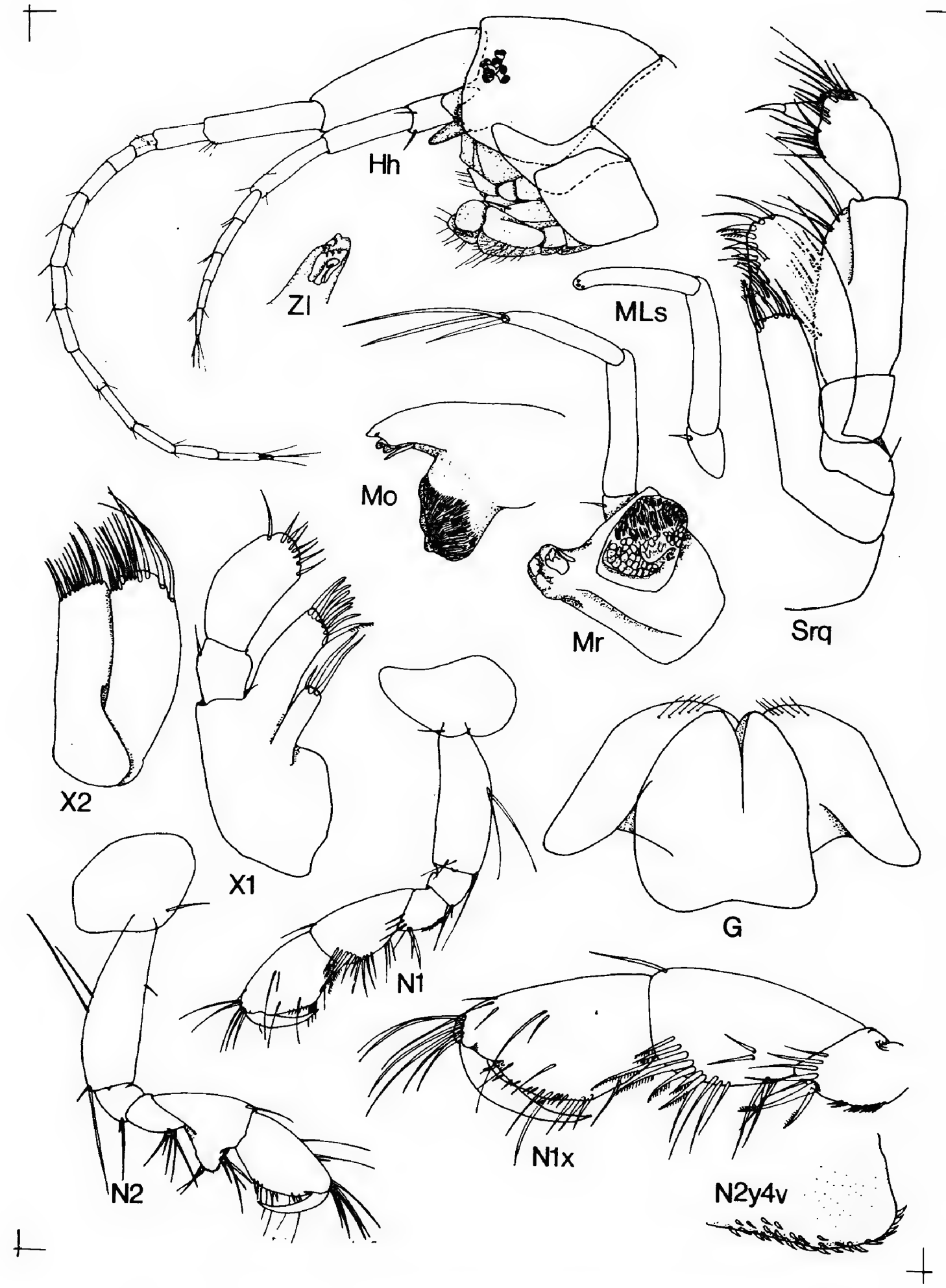

FIG 1. *Netamelita barnardi*, new species, holotype, male, 3.46 mm.

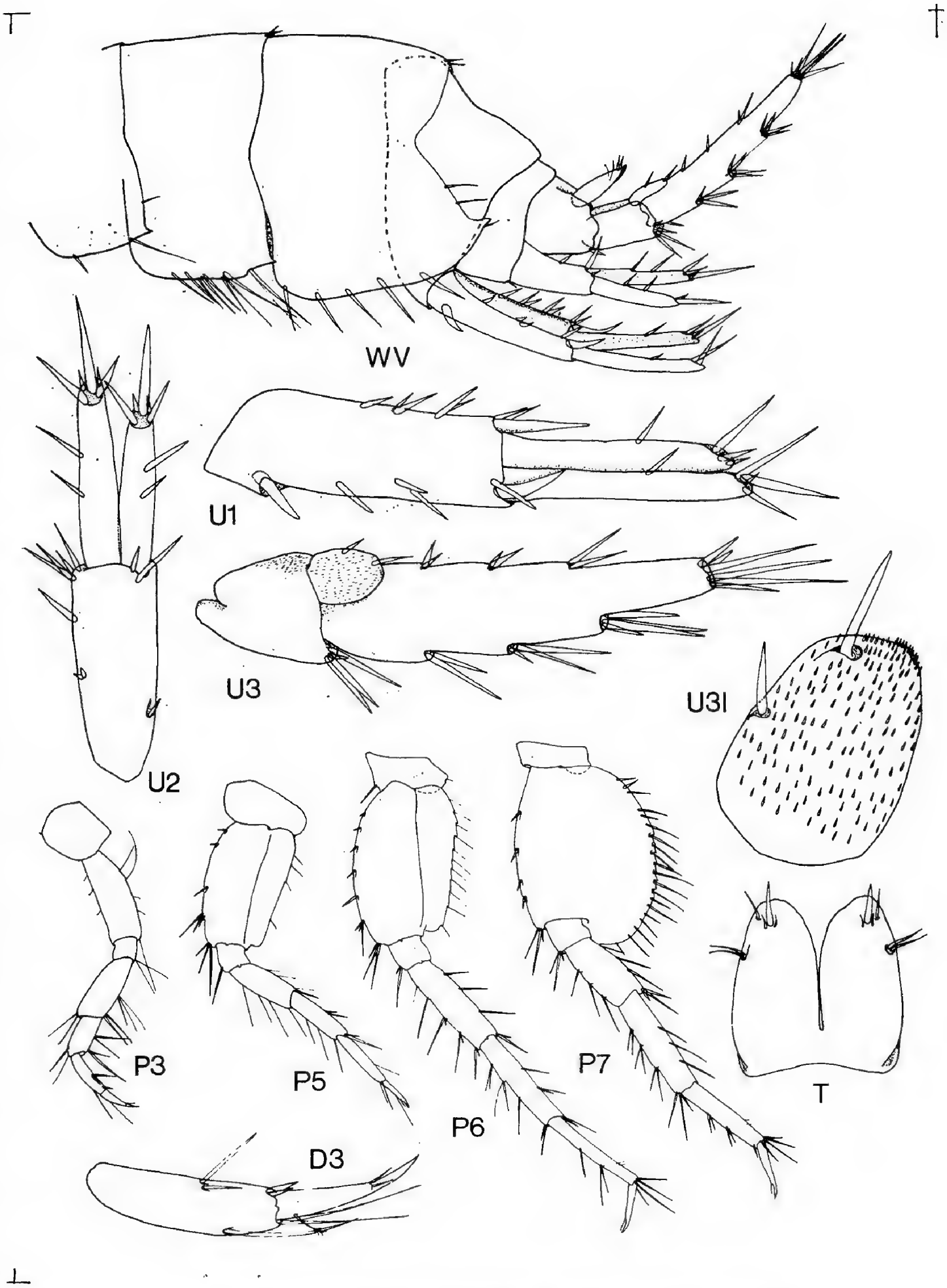

FIG 2. *Netamelita barnardi*, new species, holotype, male, 3.46 mm.

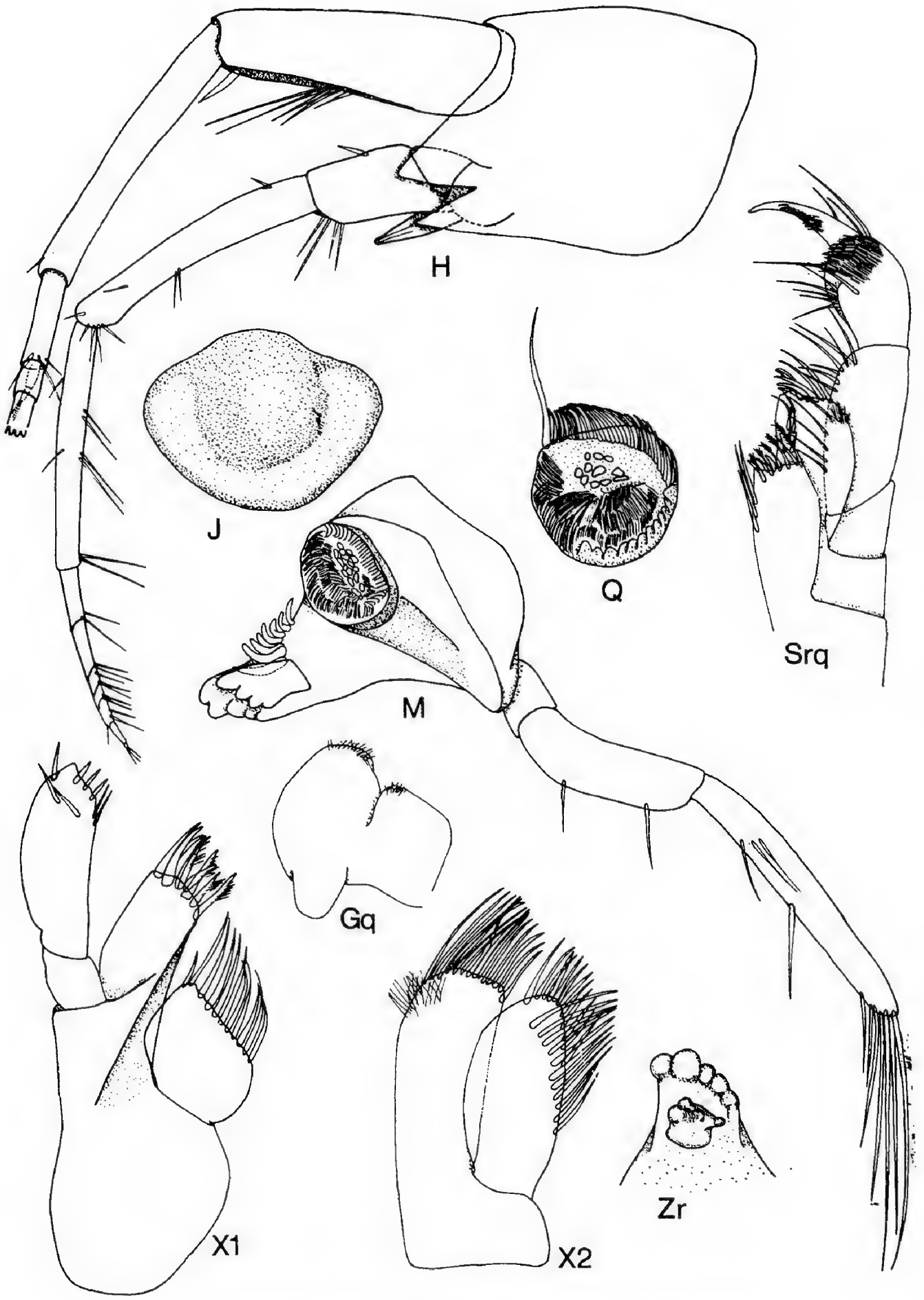

Fig. 3. *Eriopisa incisa*, new species, holotype, male 4.27 mm.

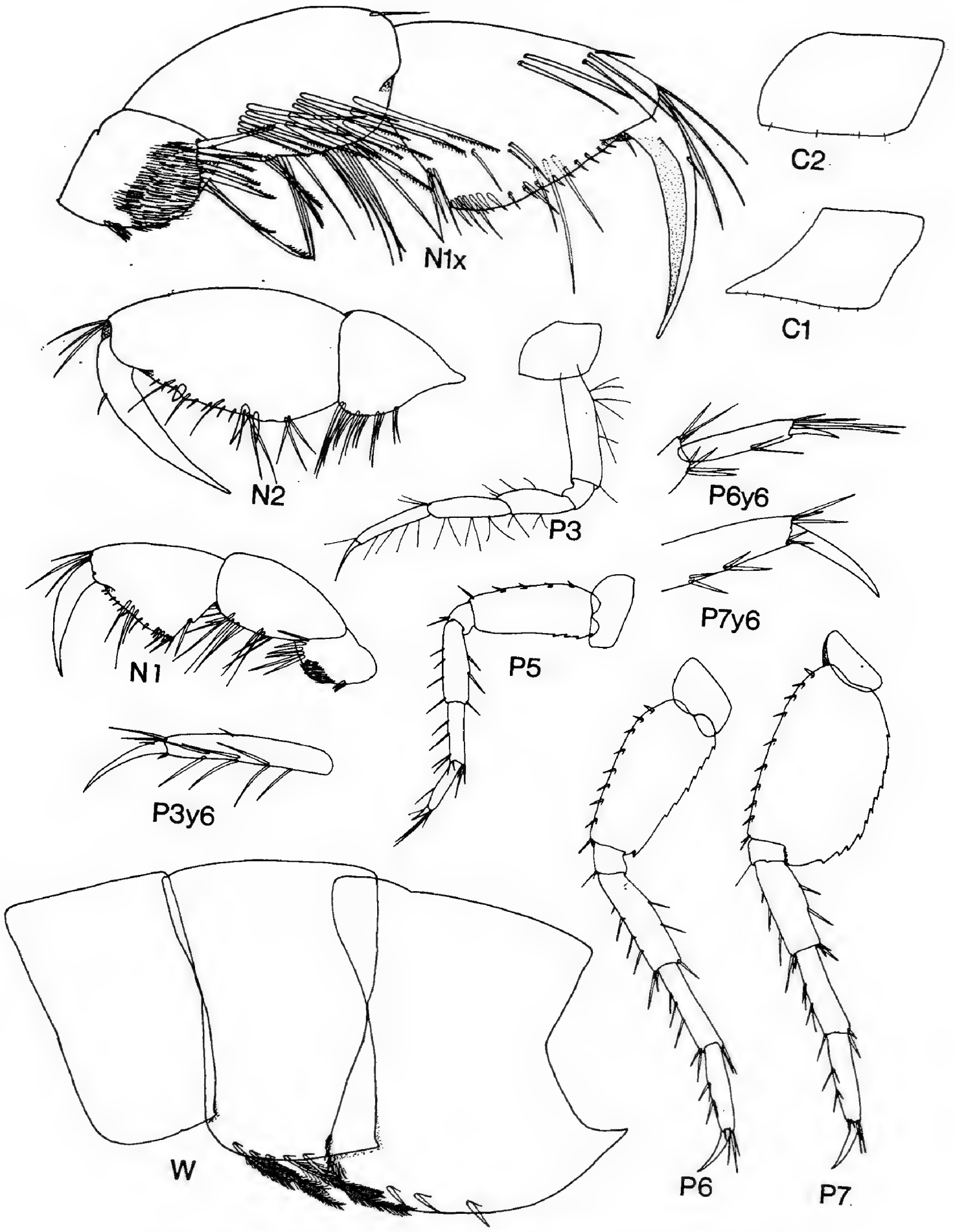

FIG. 4. *Eriopisa incisa*, new species, holotype, male, 4.27 mm.

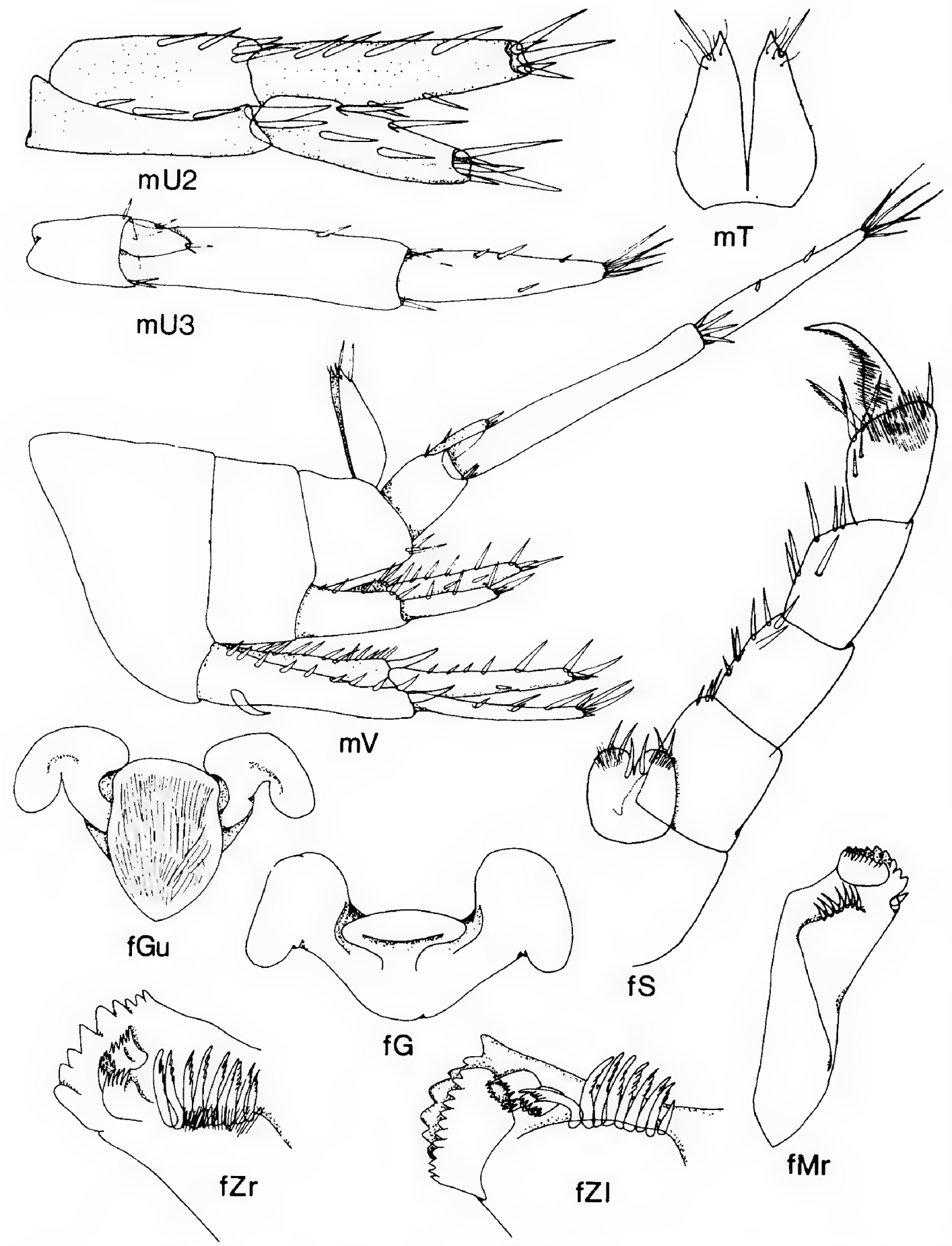

FIG 5. *Eriopisa incisa*, new species, holotype, male, 4.27 mm. m = male holotype *Parametopella texensis*, new species, holotype, female, 3.35 mm. f = female holotype.

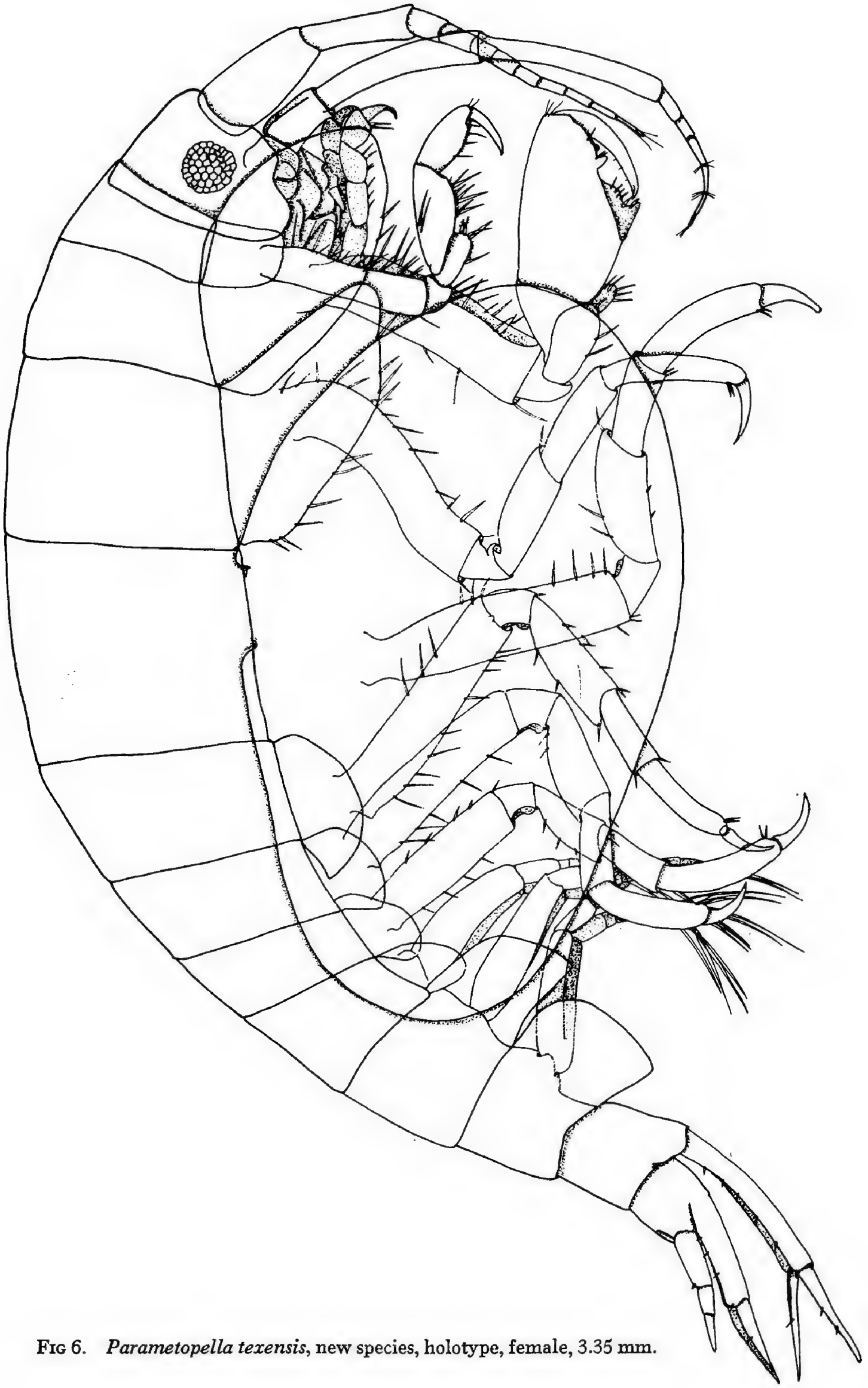

FIG 6. *Parametopella texensis*, new species, holotype, female, 3.35 mm.

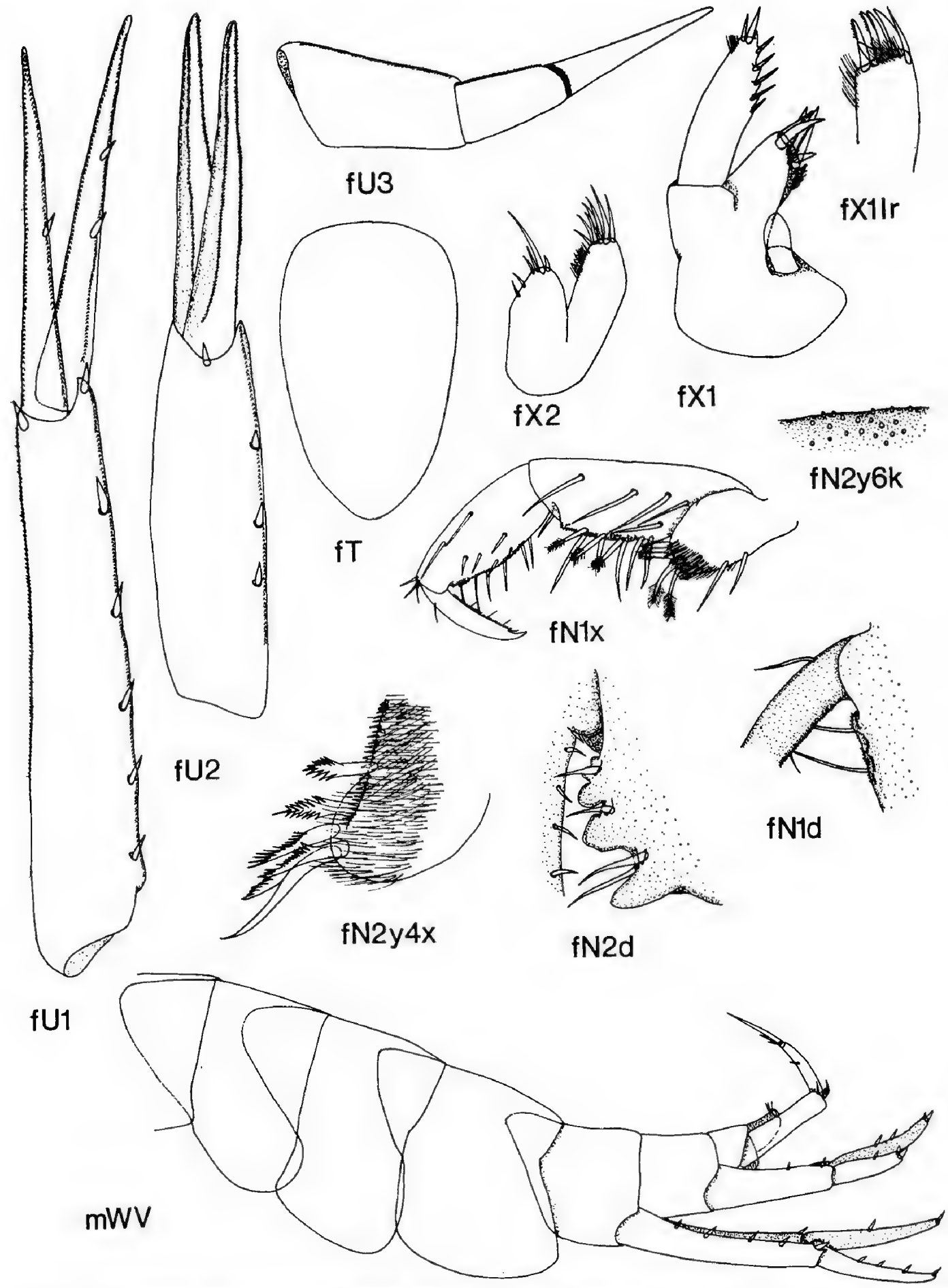

FIG 7.—*Parametopella texensis*, new species holotype, female, 3.35 mm. f = female holotype *Photis macromanus*, new species, holotype, male, 2.19 mm. m = male holotype.

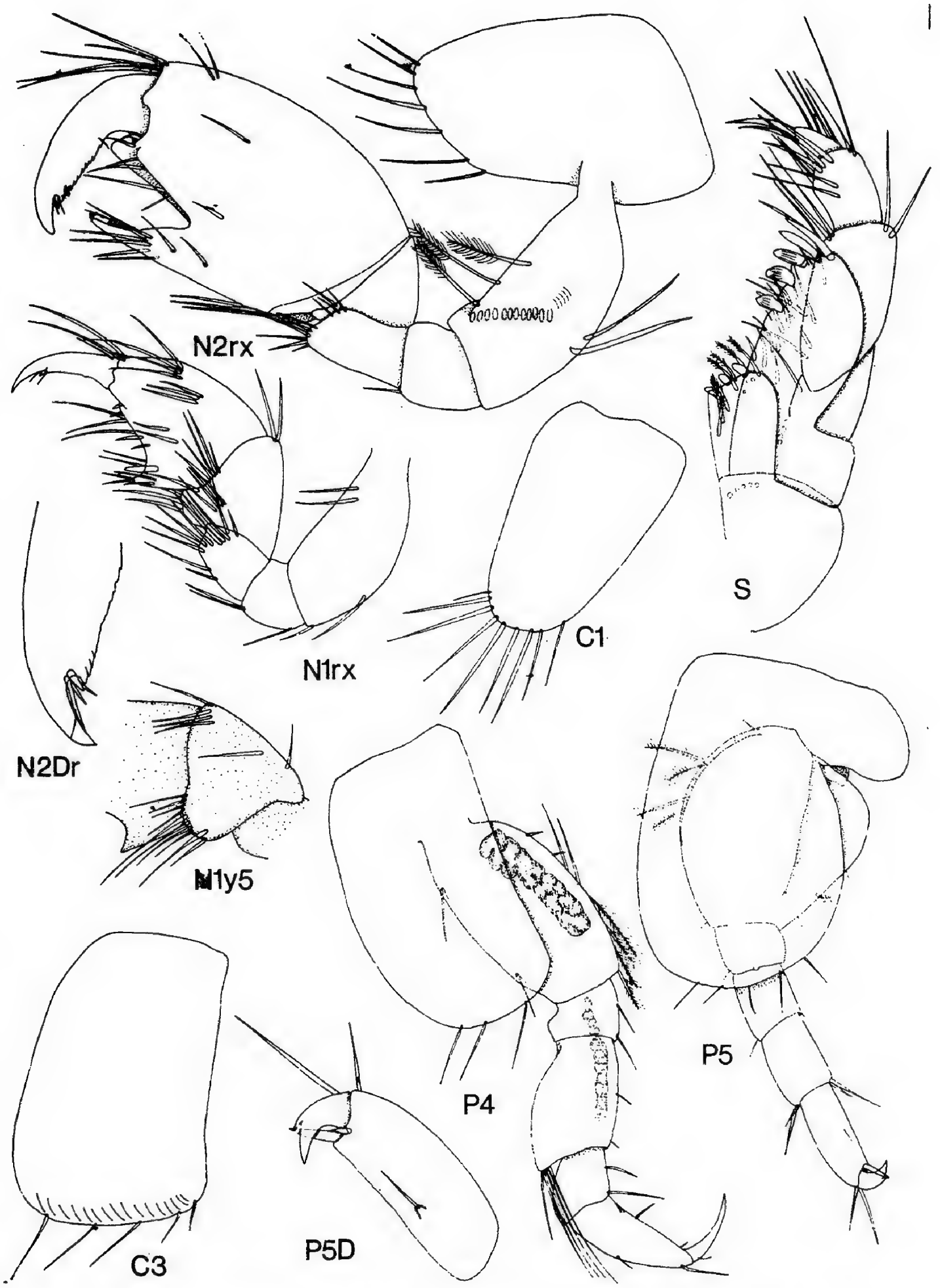

FIG 8. *Photis macromanus*, new species, holotype, male, 2.19 mm. D = dactyl of gnathopod.

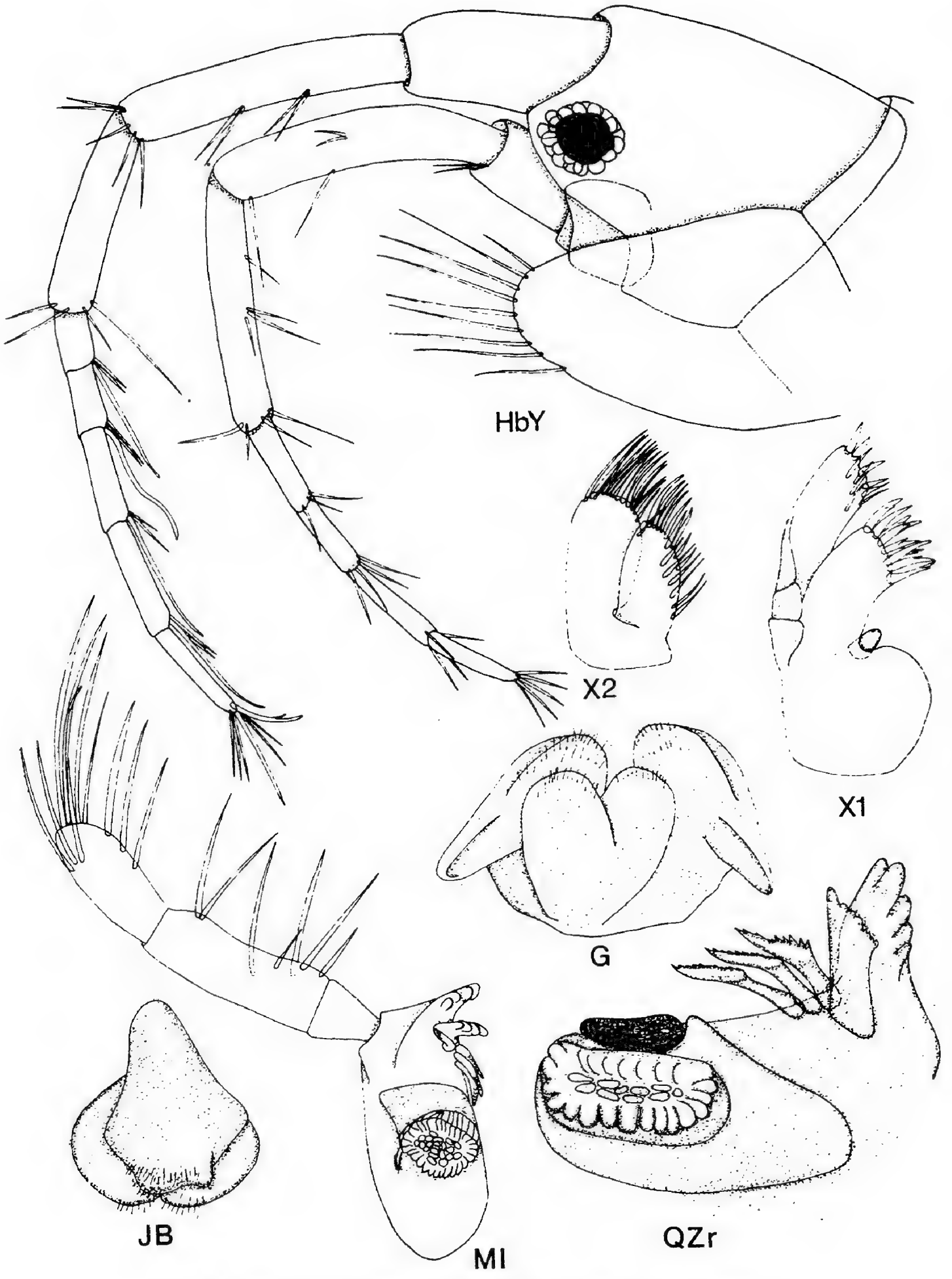

FIG. 9. *Photis macromanus*, new species, holotype, male, 2.19 mm.

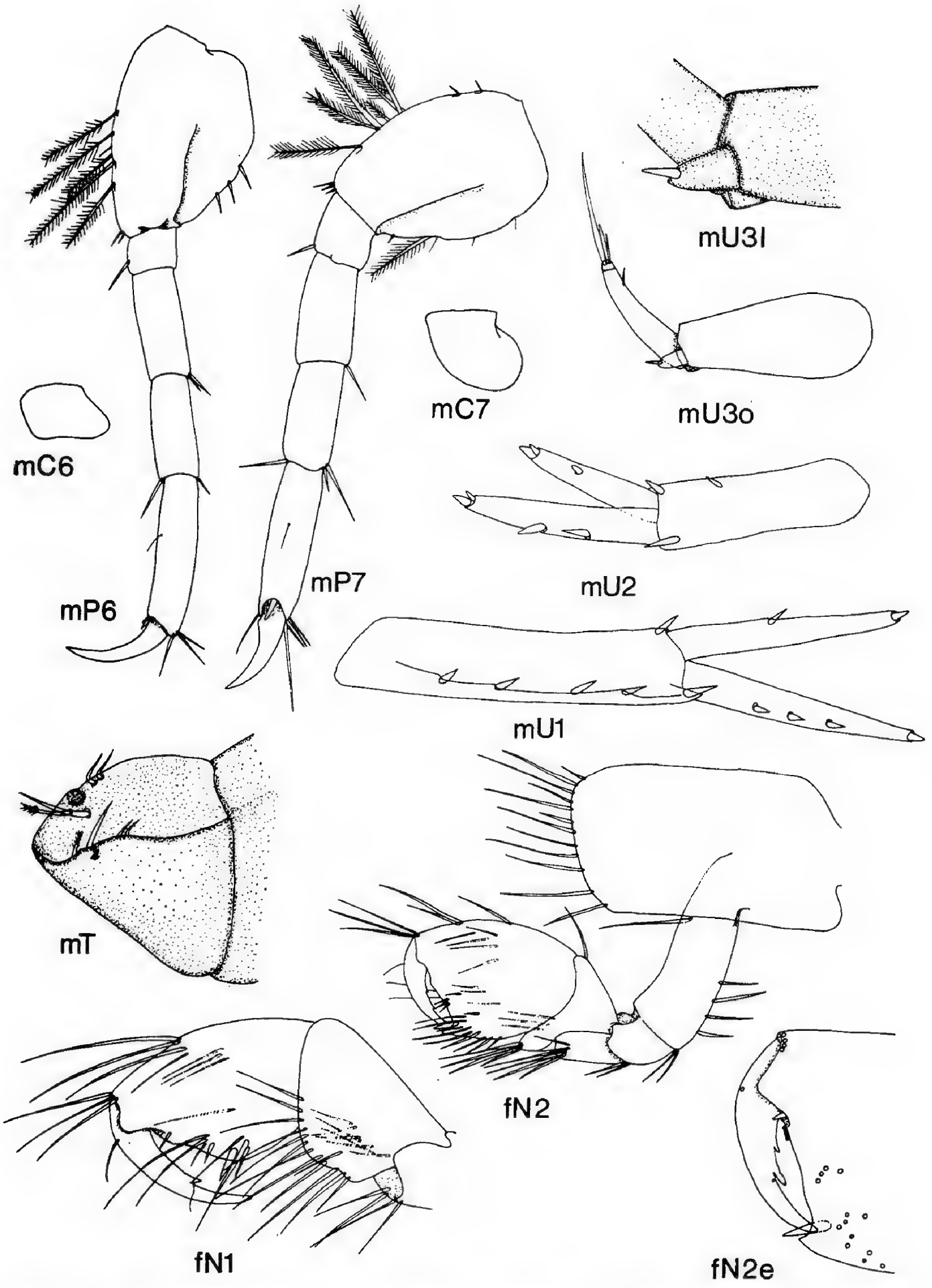

FIG. 10. *Photis macromanus*, new species, holotype, male, 2.19 mm. m = male holotype, f = allotype, female, 2.97 mm.

SCOLOPLOS TEXANA: A NEW ORBINIID POLYCHAETE FROM SOUTH TEXAS, WITH NOTES ON THE RELATED SPECIES *SCOLOPLOS TREADWELLI* EISIG

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University of Texas Marine Science Institute Contribution No. 255.

ABSTRACT

A new species of orbiniid polychaete was discovered during a survey of Corpus Christi and Redfish Bays in South Texas. A description is given, and information on its location and habitat. A comparison with the related species, *Scoloplos treadwelli* Eisig is made.

INTRODUCTION

A benthic survey of Corpus Christi, Nueces, Redfish, Copano and Aransas Bays in South Texas was initiated in October 1972. Funding was provided by the City of Corpus Christi through the Texas Water Development Board. Sediment samples were collected monthly from October 1972 through May 1975 using a Petersen grab. All organisms retained on a 0.5 mm mesh sieve were examined, identified and counted. In the course of this study, a previously undescribed polychaete belonging to the family Orbiniidae was discovered at five stations in Corpus Christi Bay and one station in Redfish Bay. The holotype and eleven paratypes are deposited in the Smithsonian Institution (USNM), four specimens are in the Allan Hancock Foundation in Los Angeles, California (AHF), and the remaining specimens are retained by the first author (NJM).

The closely related orbiniid, *Scoloplos treadwelli* Eisig is reviewed, based on a reexamination of the types and additional specimens deposited in the Allan Hancock Foundation (AHF), American Museum of Natural History (AMNH), Smithsonian Institution (USNM) and the Zoologische Museum Amsterdam (ZMA).

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SYSTEMATICS

Family: ORBINIIDAE
Subfamily: Orbiniinae Hartman, 1957
Genus: *Scoloplos* (*Scoloplos*) Blainville, 1828
Scoloplos (*Scoloplos*) *texana* sp. nov.

(Figures 1–4)

Scoloplos treadwelli Augener, 1934: 68 (part). Not Eisig 1914.

Material examined—TEXAS: Corpus Christi Bay: Sta. 122–6, 27° 48′38″N, 97° 20′17″W, April, August 1974, 4.8–5.0 m, holotype (USNM 52729) and 2 paratypes (USNM 52732). Sta. 127–2, 27° 51′17″N, 97° 15′57″W, May, June, July, October 1974, 4.2–4.7 m, paratype (USNM 52730) and 3 specimens (NJM). Sta. 127–6, 27° 46′32″N, 97° 17′41″W, June 1973, 4.7 m, 1 specimen (NJM). Sta. 142.6, 27° 45′48″N, 97° 14′10″W, March 1974, 4.8 m, paratype (USNM 52731) and 2 specimens (NJM). Sta. 147–1, 27° 49′00″N, 97° 08′22″W, March 1973, 3.1–3.3 m, 2 paratypes (USNM 52733) and 3 specimens (1 is a posterior fragment) (NJM). Redfish Bay: Sta. 152–2, 27° 52′20″N, 97° 07′03″W, December 1973, February, March, May 1974, 1.6–2.3 m, 5 paratypes (USNM 52734), 4 specimens (AHF) and 6 specimens (NJM). NE COLUMBIA: Rio Hacha, 6 m, *Chazalie*, 2 March 1896, 1 specimen (ZMA 2637, mixed with *S. treadwelli* by Augener, 1934).

Description:—The length ranges from 4 mm (18 segments) to 25 mm (70 segments), with maximum width 1.66 mm without parapodia. The color (in 70% isopropanol) appears pinkish-white, with dark brown dorsal bars on the first few (1–3) abdominal segments and faint bars on succeeding segments in some specimens. Dorsal and ventral blood vessels appear brown.

The number of thoracic segments ranges from 11 to 20. The thorax is markedly inflated and increases only slightly in width from the prostomium to mid-thorax, then decreases slightly to the beginning of the abdomen (Fig. 1). The abdomen is cylindrical, tapering posteriorly.

The prostomium is bluntly triangular, without appendages or eyes. The peristomium is apodous and achaetous, and consists of a single ring (Fig. 2). The proboscis is a soft eversible pouch (Figs. 1 and 2).

Branchiae begin on the 2nd to 4th abdominal segment as large, simple compressed lobes. Except for the first few (3–5), the lateral margins are conspicuously fimbriated for 2/3 of their length, with a smooth compressed distal tip (Fig. 4).

The thoracic notopodia have simple cirriform postsetal lobes, inconspicuous at first, but large and obvious after setiger 5 (Fig. 3). The abdominal notopodia are similar but larger and shifted to a more dorsal position (Fig. 4).

The thoracic neuropodia are simple low ridges without ventral subpodial or podial lobes or fringe. The abdominal neuropodia terminate in a bulbous lobe

supported by a single embedded aciculum (Fig. 4). No interramal cirri are present. No dorsal ciliated ridges or ventral pads were seen.

Thoracic notosetae consist of crenulate capillaries; abdominal notosetae are the same, with a few (1–3) furcate setae in some posterior segments. The notosetae are arranged in fascicles anterior to the cirriform postsetal lobes. Thoracic neurosetae consist of a single row of 5–9 dark brown acicular spines, with entire, somewhat curved tips, plus 1 to several capillaries set along the dorsal edge of the row (Fig. 3). Abdominal neurosetae consist only of crenulate capillaries (Fig. 4).

Two cirriform anal cirri are present.

Habitat:—*Scoloplos texana* was found on clay or muddy sand with slight to large amounts of shell, in depths of 1.6 to 5.0 meters. Salinities ranged from 15.8 to 32.7 ‰, is dissolved oxygen from 5.6 to 9.9 mg/l, and temperature from 17.0 to 30.0°C (Table 1).

TABLE 1

Environmental parameters associated with *Scoloplos texana* in Corpus Christi and Redfish Bays, South Texas.

Station		Depth (m)	Salinity o/oo	D.O. (mg/l)	Temp. (°C)	Sediment Type
122-6	Apr 74	5.0	25.5	7.5	21.2	Shelly Clay
	Aug 74	4.8	32.7	5.9	30.0	
127-2	May 74	4.7	22.5	6.0	28.0	Shelly Clay
	June 74	4.2	26.4	5.6	27.6	
	July 74	4.2	28.5	5.7	28.0	
	Oct 74	4.2	25.8	6.0	22.0	
127-6	June 73	4.7	29.2	5.8	27.0	Slightly Shelly Clay
142-6	Mar 74	4.8	26.8	7.0	22.9	Slightly Shelly Clay
147-1	Mar 73	3.3	27.0	7.8	21.0	Slightly Shelly, Muddy Sand
152-2	Dec 73	1.8	15.8	9.9	17.0	Shelly Muddy Sand
	Feb 74	1.6	25.4	8.0	19.0	
	Mar 74	2.1	21.7	9.2	22.1	
	May 74	2.3	22.5	6.0	28.0	

Scoloplos treadwelli Eisig 1914

Aricia cirrata Treadwell, 1901: 201, figs 54–57. (Homonym). Not Ehlers, 1897. *Scoloplos treadwelli* Eisig, 1914: 405 (New name for *Aricia cirrata* Treadwell, preoccupied).—Augener, 1927: 69; 1934: 68 (part).—Hartman, 1957: 283.

Scoloplos cirrata—Treadwell, 1931: 4.

Material examined.—PUERTO RICO: Mayaguez Harbor, 22–23, 177–220 m, *Fish Hawk* sta 6061, 6066, 6067, 20 January 1899, 3 syntypes of *Aricia cirrata* (USNM 16065–7). JAMAICA: Montego Bay, July 1921, A. L. Treadwell, collector, 3 specimens (AMNH 2020, as *Scoloplos cirrata* by Treadwell, 1931). CURAÇAO: Spaansch Water, 17 April 1920, 1 specimen (ZMA 1312, identified by Augener, 1927). NE COLUMBIA: Rio Hacha, 6 m, *Chazalie,* 2 March 1896, 1specimen (ZMA 1313, identified by Augener, 1934). PACIFIC SIDE MEXICO: off Acapulco, 16° 40′37″N, 99° 55′30″W, 24 m, *Velero* sta 2597–54, 1 February 1954, 2 specimens (AHF F2104, identified by Hartman, 1957).

The specimens from Acapulco are in poor condition, and while agreeing in all major characters, are omitted from the following brief description.

The prostomium is acute and lacks eyes. The anterior thorax is narrow, widening rapidly so that the posterior thorax is, in some specimens, much wider than the anterior portion. Maximum thoracic width ranges from 1.6 to 3.5 mm. The prostomium is followed by an apodous, achaetous peristomium. The pharynx is a soft, eversible pouch.

The number of thoracic segments ranges from 14 to 22. The thorax is flattened dorsally, but somewhat rounded ventrally.

Branchiae begin on the penultimate thoracic, ultimate thoracic or first abdominal segment. They appear similar to those of *S. texana.*

The thoracic and abdominal notopodia and neuropodia are as described for *S. texana.* Treadwell (1901) referred to the thoracic notopodial postsetal lobes as "dorsal carri".

Notosetae and neurosetae are similar to those found in *S. texana.* The acicular neurosetae regularly occur in double rows in the first 7–11 thoracic setigers, followed by irregular rows for 1–3 segments and single rows thereafter. Of the specimens examined, only 2 did not have neurosetae in double rows. The acicular neurosetae are lighter in color than those of *S. texana,* anteriorly often light yellowish brown, becoming dark brown posteriorly.

DISCUSSION

Hartman (1957) provided a comprehensive review of the family Orbiniidae and established two subfamilies: Orbiniinae and Protoariciinae. Both *S. texana* and *S. treadwelli* belong to the Orbiniinae based on the following characteristics: one achaetous peristomial segment (as opposed to two) and an eversible epithelial pharynx (as opposed to muscular and non-eversible).

Within the genus *Scoloplos,* the location of the first pair of branchiae after setiger 10 and the presence of embedded rather than projecting acicula in the abdominal neuropodia refer the specimen to *Scoloplos* (*Scoloplos*) Blainville,

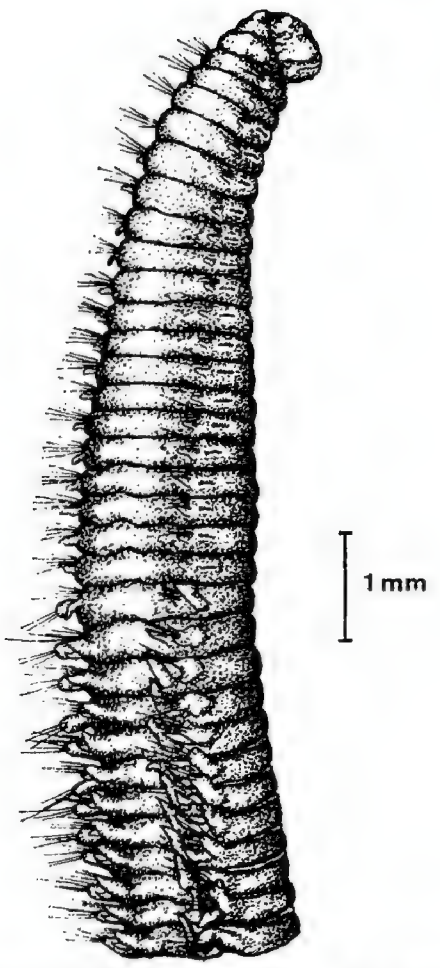

FIG. 1. *Scoloplos texana*, proboscis extended, dorso-lateral view.

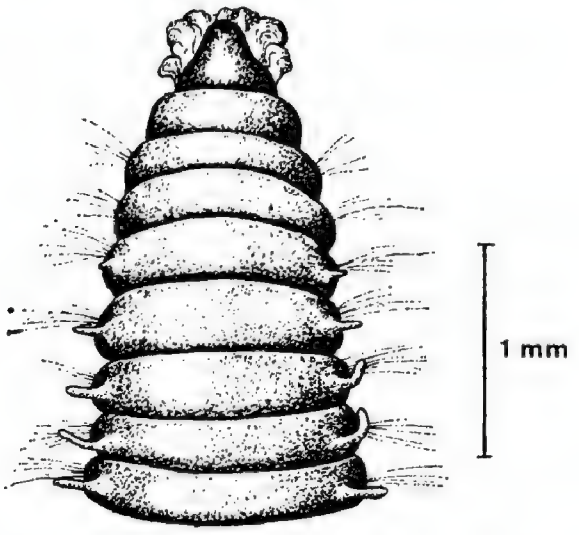

FIG. 2. *Scoloplos texana*, proboscis extended, dorsal view of prostomium and part of thorax.

rather than to *Scoloplos* (*Leodamas*) Kinberg (Day 1973). Pettibone (1957) separated the two subgenera on the basis of the presence or absence of papillae on the postsetal lobe of the neuropodia. Lack of such papillae would refer both *S. texana* and *S. treadwelli* to *S.* (*Leodamas*). Hartman (1948, 1957) considered the character of the embedded vs. projecting acicula in the abdominal neuropodia as the most important in separating the two subgenera, while Day (1973) emphasized the appearance of the first pair of branchiae. Following the latter two authors, the species discussed here belong to *S.* (*Scoloplos*).

The major differences between *S. texana* and *S. treadwelli* are that the former never has branchiae beginning on the thorax (Table 2), the thorax is definitely

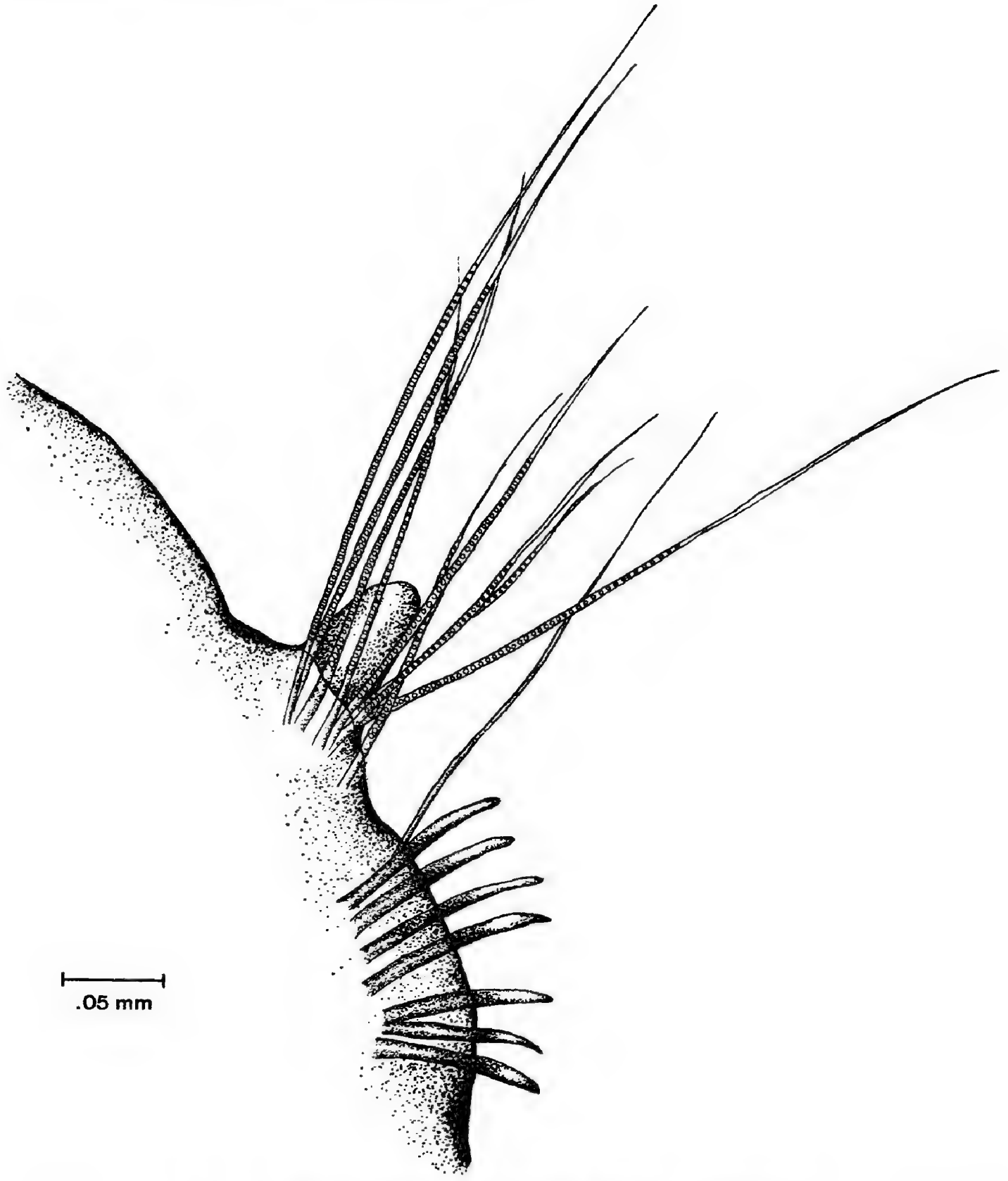

FIG. 3. *Scoloplos texana*, tenth thoracic setiger, anterior view.

inflated, and the thoracic neurosetae never occur in double rows. *S. treadwelli* has branchiae beginning in the thorax or abdomen, a dorsally flattened thorax, and often double rows of thoracical neurosetae. Minor differences between the two species include the shape of the prostomium, changes in the width of the thorax, and differences in intensity of color of the thoracical neurosetae.

ACKNOWLEDGMENTS

The authors particularly wish to thank Dr. Kristian Fauchald of the Allan Hancock Foundation, Los Angeles, California and Dr. Marian Pettibone of the Smithsonian Institution, Washing-

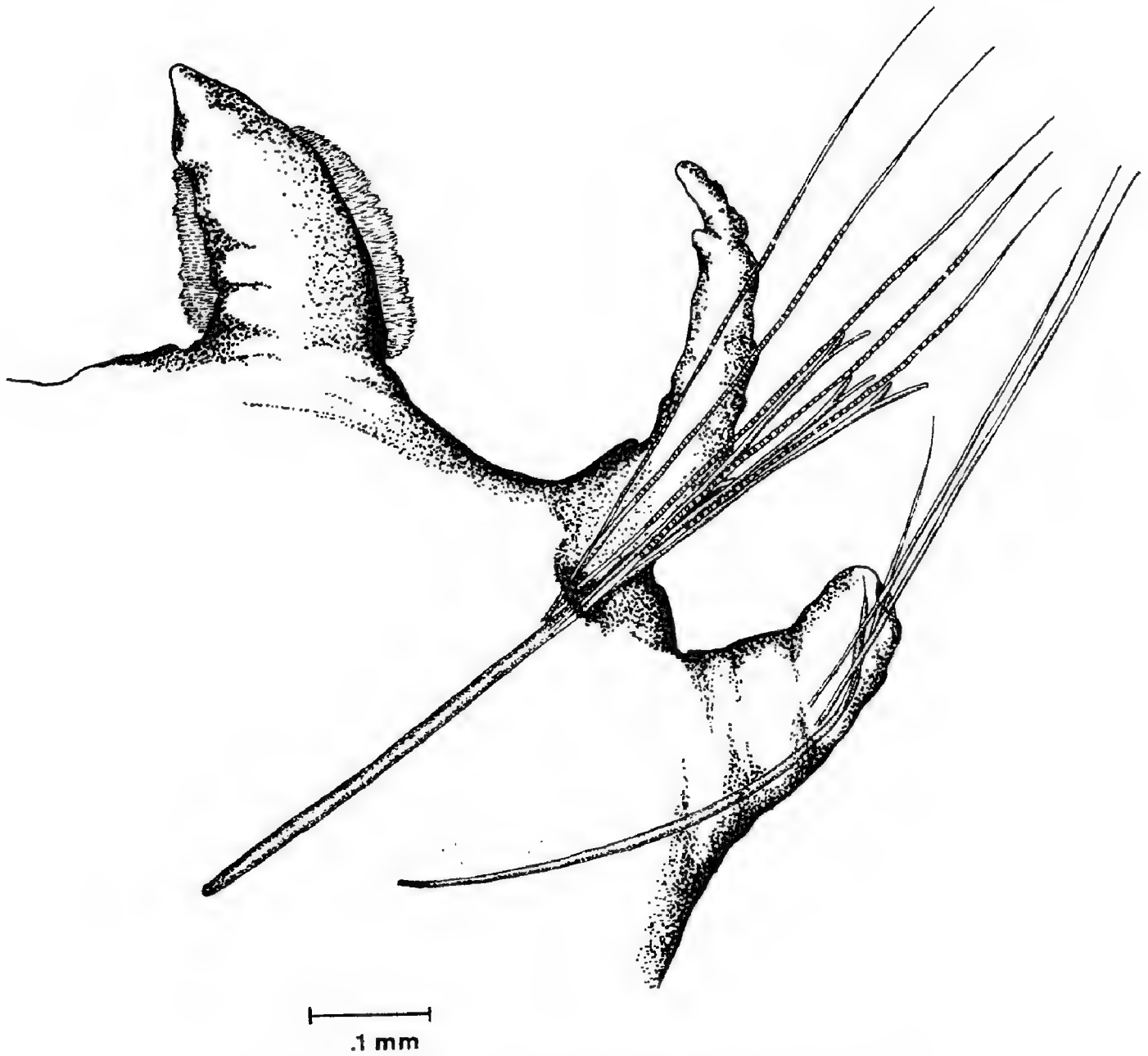

FIG. 4. *Scoloplos texana*, 58th setiger, anterior view.

ton, D.C. for their invaluable advice and assistance in the preparation of this manuscript. Dr. Pettibone, Dr. Ernest Kirsteuer of the American Museum of Natural History, New York, and Dr. J. van der Spoel of the Zoologische Museum, Amsterdam made it possible for the first author to examine specimens of *S. treadwelli*. Mark Poff of UTMSL offered helpful comments. Allen Dixon did the illustrations. The City of Corpus Christi and the TWDB provided funds without which the original study would not have been made.

LITERATURE CITED

AUGENER, H. 1927. Polychaeten von Curaçao. *Bijdr. Dierk.* **25**:39–82.

————. 1934. Polychaeten aus den zoologischen museum von Leiden und Amsterdam. IV. Schluss. *Zool. Meded. Leiden.* **17**:67–160.

DAY, J. H. 1973. New polychaeta from Beaufort, with a key to all species recorded from North Carolina. *NOAA Tech Rept. NMFS Circ.* **375**. 140 pp.

EISIG, H. 1914. Zur Systematik, Anatomie und Morphologie der Ariciiden nebst Beitragen zur generellen Systematik. *Mitt. Zool. Stn. Neapel* **21**:153–600.

HARTMAN, O. 1948. The marine annelids erected by Kinberg, with notes on some other types in the Swedish State Museum. *Ark. Zool. Stockholm.* **42**A, No. 1, 137 pp.

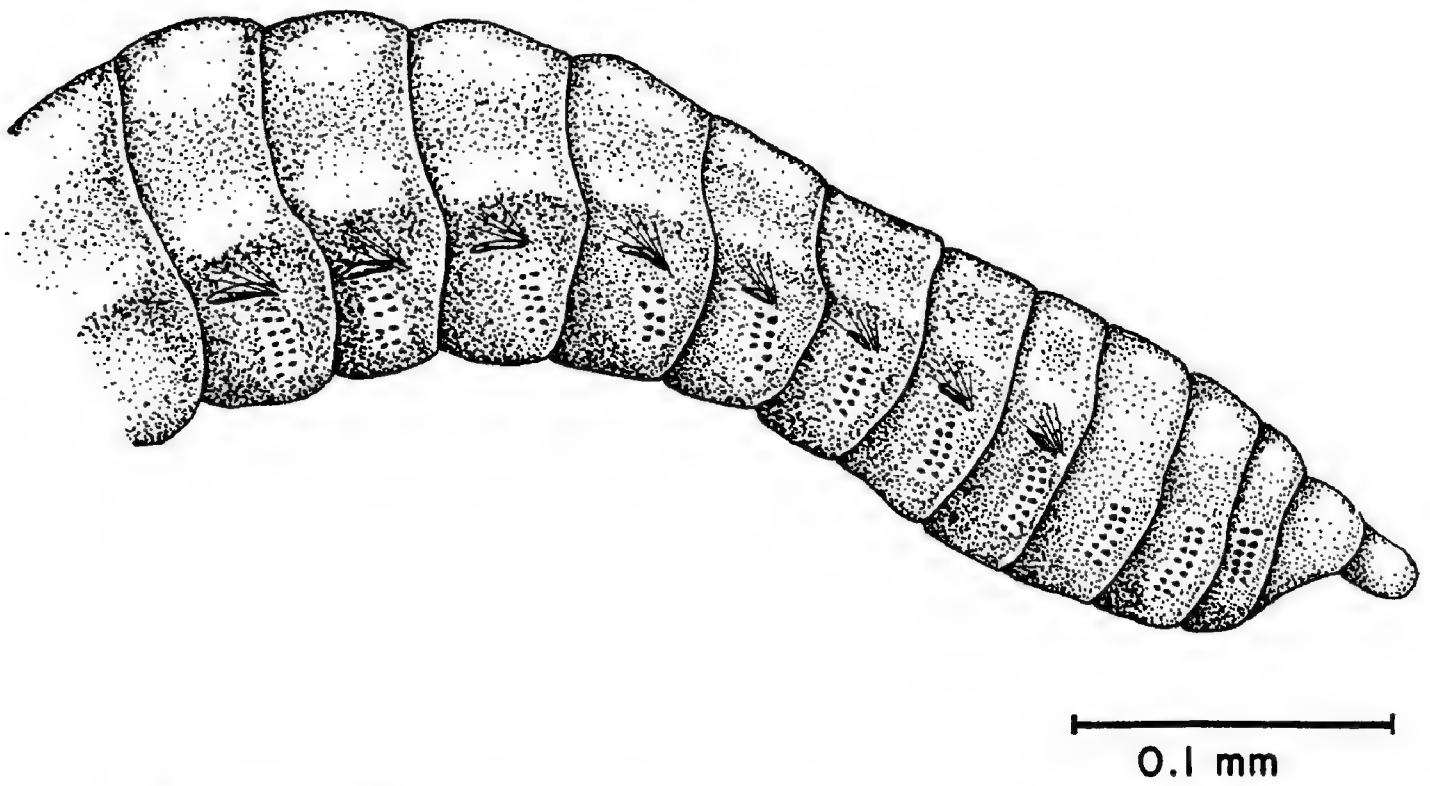

FIG. 5. *Scoloplos treadwelli*, anterior end, lateral view showing double rows of acicular neurosetae.

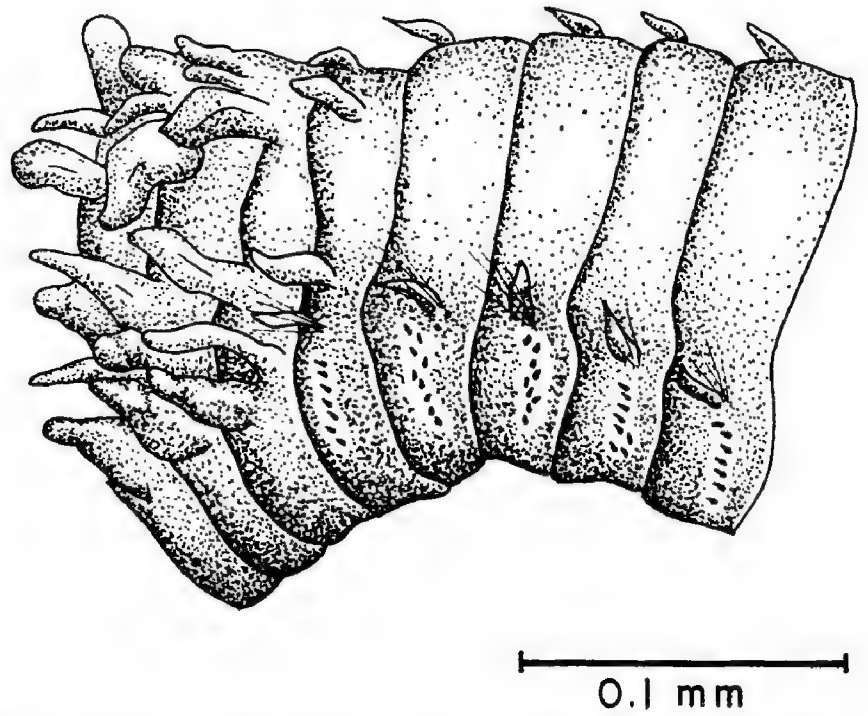

FIG. 6. *Scoloplos treadwelli*, dorso-lateral view of last few thoracial and first few abdominal setigers, showing start of branchiae on last thoracical setiger. Setae removed.

———. 1957. Orbiniidae, Apistobranchidae, Paraonidae and Longosomidae. *Allan Hancock Pacif. Exped.* **15**(3):211–393.

PETTIBONE, M.H. 1957. North American genera of the family Orbiniidae (Annelida: Polychaeta) with descriptions of new species. *J Wash. Acad. Sci.* **47**(5):159–167.

TREADWELL, A. 1901. The polychaetous annelids of Porto Rico. *Bull U.S. Fish Commn.* **20**(2):181–210.

———. 1931. New species of polychaeteous annelids from California, Mexico, Porto Rico and Jamaica. *Am Mus. Novit.* No. **482**:1–7.

TABLE 2

Number of thoracic setigers and position of first pair of branchiae on *S. treadwelli* and *S. texana*.

Species, Location		No. of Thoracic Setigers	Branchiae Start Setiger No.
Scoloplos treadwelli			
Puerto Rico (USNM)	1	16	16
	2	14	13
	3	19	20
Montego Bay (AMNH)	1	21	21
	2	20	21
	3	20	21
Rio Hacha (ZMA)		22	23
Curacao (ZMA)		19	19
Scoloplos texana			
Sta. 122–6 (USNM 52729)		19	22
Sta. 127–2 (USNM 52730)		19	21
Sta. 142–6 (USNM 52731)		17	21
Sta. 122–6 (USNM 52732)	1	19	23
	2	19	22
Sta. 147–1 (USNM 52733)	1	18	21
	2	20	23
Sta. 152–2 (USNM 52734)	1	18	20
	2	18	20
	3	16	18
	4	14	17
	5	14	17
Sta. 152–2 (AHF)	1	18	21
	2	15	18
	3	16	19
	4	11	14
Sta. 127–2 (NJM)	1	18	20
	2	16	18
	3	11	13
Sta. 127–6 (NJM)		16	18
Sta. 142–6 (not counted)			
Sta. 147–1 (NJM)	1	17	20
	2	18	21
Sta. 152–2 (NJM)	1	14	16
	2	12	15
	3	13	15
	4	12	15
	5	10	12
	6	13	16

SALINITY STRESSES, METABOLIC RESPONSES AND DISTRIBUTION OF THE COASTAL SPOTTED SEATROUT, *CYNOSCION NEBULOSUS*[1]

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ABSTRACT

Standard routine and maximum sustained respiratory metabolic rates at 28°C, and over a salinity range of 10 to 45 ppt, demonstrated that the optimal salinity was about 20 ppt, for the spotted seatrout, *Cynoscion nebulosus*, in south Texas coastal waters. At about 20 ppt salinity, standard (maintenance) metabolism was at a minimum, while active metabolism, scope for activity, and swimming velocities were at a maximum. Multiple regression equations relating all the variables to metabolic rates could be used to calculate expected active rates that agreed well with active rates actually observed at the different salinities. The metabolic rate equations between successive 5 ppt salinity intervals had a very high statistical precision, the weight-metabolism coefficients were consistently near unity, and the swimming-metabolism coefficients tended to be highest at the optimal salinity of about 20 ppt and lowest at the 10 and 45 ppt extremes. Fish in poor condition had greatly depressed metabolism and swimming rates. The routine (operational) metabolism rates were at a swimming rate of about 1 length sec^{-1} for all salinities and were about double the corresponding standard rates. The maximum sustained metabolic levels at about 10 and 45 ppt were reduced to the routine level, indicating that the species is operationally limited below 10 ppt and above about 45 ppt, a fact observed from catch data in the widely ranging salinities of various Texas coastal waters. The data agree with zoogeographic salinity optimization and with general population and ecosystem theories of optimization, which are based on energetics. It is suggested that similar metabolic data over a range of natural stresses like salinity can be used as a baseline to assess stresses in general.

INTRODUCTION

The purpose of this study is to evaluate the natural salinity range of *Cynoscion nebulosus*, the spotted seatrout, in terms of metabolic responses. This species, which is commercially and recreationally important, occurs abundantly over a a wide range of coastal and estuarine waters from southeastern U. S. through the U. S. and northwestern Mexican Gulf of Mexico regions.

Because these regions often have wide salinity fluctuations and because freshwater diversions and wide fluctuations in rainfall can alter coastal salinity re-

[1] University of Texas Marine Science Institute Contribution No. 251.

gimes radically, it is important to know what biological processes can be used to evaluate salinity regimes for the various organisms. Because respiratory metabolism is a generalized process, it provides a basis for the evaluation of standard (maintenance). routine (operational), and maximum sustained metabolism in relation to salinity or other stresses. This study involves the rationale that the metabolic scope for activity (Fry 1947) is at a maximum at an optimal salinity. Scope for activity is defined as the difference between the oxygen consumption rate per unit weight, at maximum sustained swimming velocity and the rate at the minimal maintenance, or standard, level. Oxygen consumption rates, which are expressed as regressions on body weight or as rates per unit weight, have great general utility when converted to energy, work or power units either in population or in ecosystems studies.

Both theoretical and empirical studies indicate that for a given energy input, any biological system under stress tends toward reduced output when compared to an unstressed system. Since Fry's (1947) evaluation of metabolic scope, numerous authors have extended the concept of metabolic scope to various species and environmental circumstances. Brett (1958, 1964, 1965, 1971, 1976), Brett and Glass (1973) and Brett *et al.* (1969) have extended the concept to actively swimming sockeye salmon over a variety of environmental and feeding conditions especially with reference to optimal swimming performance, ration, assimilation, growth, etc. at optimal temperatures. Fry (1971) reviews much of the research pertinent to fishes and discusses the concept in terms of lethal, controlling, limiting and directive factors. More recently Webb (1975) has reviewed several important features of swimming energetics and hydrodynamics that are important for the interpretation of maximum scope under optimal environmental circumstances.

For a normal, lightly fasted fish, the scope for maximum sustained activity is expected to decrease under stress either by raising the standard metabolism (if the fish is adapted to expend such energy), by reducing the level of active metabolism, or by both expectations (Fry 1971). For a fish that is losing weight or suffering from some degree of morbidity, the expectation is that maintenance requirements are not being met so that the levels of standard metabolism would be reduced temporarily, while the maximum active metabolic rate would be more or less severely reduced. Metabolic rates at maximum swimming activity require 4–8 times standard rates for many fishes (Randall 1970), but such rates are not continuously possible for most species. Many fish in nature are characterized by a "routine" metabolism that lies between the standard and maximum activity levels.

For slightly fasted fish in the laboratory, the routine operational metabolic rate requirements would include standard metabolism, plus foraging (routine swimming activity), plus possibly some costs for assimilation and other functions not entirely eliminated by fasting. Fry (1957, 1971) and Winberg (1956) review much of the literature on metabolic rates, from which might be anticipated two classes of stress effects: (1) Under natural stress gradients, like salinity in this study, the point at which maximum active metabolism was depressed to the routine level would be the limiting point along the stress gradient for general

survival; and (2) Under any kind of stress that would depress the routine level, there would be an inhibition of the normal foraging and assimilation energy requirements for survival. In the second class, it is known that chronic, low level pollution stresses depress the routine rates for pinfish, *Lagodon rhomobodies* (Wohlschlag and Cameron 1967, Kloth and Wohlschlag 1972) in south Texas waters so that the "routine scope" is reduced. The concept of "routine scope for activity" was first utilized by Beamish (1964). Similarly, data are available to show that growth rates are also depressed in the striped mullet (*Mugil cephalus*) when routine metabolism is also depressed (Cech and Wohlschlag 1975) after prolonged warm temperatures and under both high salinity and possibly sublethal pollution stresses.

The purpose of this study then is to obtain metabolic rate measurements at standard, routine and maximum sustained swimming levels over a range of salinities that are found in the south Texas coastal waters so that an interpretation of optimal salinity requirements may be made for *Cynoscion nebulosus*. Because survival and growth problems associated with higher salinities are likely to be greatest at the end of the warmest season (Cech and Wohlschlag 1975), this study will pertain to 28° C, a normally prevailing temperature level from late spring to early autumn in the more open coastal water.

METHODS AND MATERIALS

Experimental Fish

The fish used for the routine and standard metabolism measurements were taken in the general vicinity of Port Aransas, Texas from Lydia Ann Channel late July and August 1975, where salinities were about 25 ppt and temperatures about 28° C. Virtually all the fish were taken beneath portable flood lights at night with live shrimp baited hook-and-line techniques. Fresh fish were immediately transported at night to the laboratory where they were transferred to circular tanks about 1.8 m in diameter without much salinity or temperature change. Sea water was pumped continuously through these holding tanks. For acclimation, the fish were held at $28 \pm < 1°$ C and at the desired salinity in 1.5 m diameter circular tanks, with salinities not changed more than 5 ppt over a two-day period. The fish were fed live shrimp *ad libitum*. With an initial ambient temperature of 28° C and salinity of 25 ppt, a minimum two-day acclimation at 25 ppt would ensue; for the same initial ambient conditions, a minimum of 10 days would ensue for salinity changes and acclimation before 45 ppt experiments were initiated. For the final two-day acclimation period, the fish were not fed. Sizes ranged from 45–769 g and 17.4–43.5 cm total length.

Fish for the active metabolism experiments were also taken from Lydia Ann Channel during July and August 1976 at about 28° C and 25 ppt and during September to the first week of October at the same salinity and about 25–28 C. The acclimation procedures were the same as above, but the final acclimation under fasting conditions was in an insulated circular tank equipped with a pump that circulated the water at about 10–20 cm sec^{-1}.

In both sets of experiments, the waters at higher salinities were obtained from outdoor evaporation of sea water in a large, shallow roof-top tray. De-ionized water was used for dilution of sea waters to lower salinities.

Routine Metabolism

The techniques and evaluations for measurement of routine metabolism follow Wohlschlag and Juliano (1959), Wohlschlag and Cameron (1967), Wohlschlag, *et al.* (1968) and Wohlschlag and Cech (1970). Acclimated individual fish swimming at "voluntary" speeds in an an-

nular enclosed chamber, that is immersed in the water to which the fish have been acclimated, provide the basic data on oxygen consumption rates. For this set of experiments at 28° C, salinity acclimation levels were 15, 25, 35, and 45 ppt.

Acclimated fish at each salinity level were introduced into the 42.12 l clear acrylic plastic chamber that could be rotated at whatever speeds the fish would swim by means of a variable, constant torque motor mechanism from which the chamber was suspended. The swimming track per revolution was 2 m. With a minimum of handling, each experimental fish was coaxed into the chamber through a sealable hatch. Water samples for oxygen analyses were withdrawn through a small outlet tube from the chamber; replacement water was added through an inlet tube and funnel that were supported above water level on the suspension rods from the overhead motor.

As soon as the fish had become "accustomed" to the chamber and would appear to swim consistently in a given position, rotations continued following withdrawal of the initial water sample. Revolutions were recorded by a revolution counter, which operated from the rotating suspension system. Counts (2 m per revolution) were recorded for at least three 15-min intervals, between water samplings and oxygen analyses. For very small fish, the time intervals between oxygen analyses were as long as 30 minutes. With chamber O_2 levels corrected for water withdrawn and added, a simple regression of the decline in O_2 against time provided the rate of consumption in mg O_2 hr^{-1}. At the termination of the run, data on temperature, salinity, length, weight and sex were recorded and tabulated along with mg O_2 hr^{-1} and mg O_2 $kg^{-1}hr^{-1}$, and swimming rates in cm sec^{-1} and as body lengths sec^{-1}. Ten fish at each salinity level were tested.

Oxygen measurements were by means of a Radiometer PHM-71 acid-base analyzer and an E-5046 electrode with an appropriate temperature control and calibration. Oxygen levels remained near saturation for acclimation and not lower than about 65% of saturation at the completion of individual experiments.

Active Metabolism

Experiments up to maximum sustained swimming rates at 5 ppt. salinity levels between 10 and 45 ppt were conducted in a "Blazka" type chamber (Blazka, *et al.* 1960 and as illustrated in Fry 1971). The modified design includes a cylindrical, transparent, acrylic plastic swimming tunnel 63 cm long, OD 20.32 cm, ID 19.05 cm. An impeller, powered by a 10 hp, constant torque, variable speed motor draws water through the tunnel. The motor is mounted outside a large wood and fiberglass temperature-controlled aquarium and is attached to the impeller by a shaft through a stuffing box in the rear aquarium wall that also supports the fixed portion of the Blazka chamber inside the aquarium. After reaching the impeller at the posterior end of the chamber the water is pumped back through a dome-and-cone structure and through an ID 29.2 cm acrylic plastic cylinder that surrounds the innermost swimming tunnel. From this outer cylinder the water passes through another cone-and-dome structure that reverts the flow into the inner cylinder. This structure is equipped with two "egg-crate" baffles and a 4 mm screen at the front of the swimming tunnel, which aid in "linearizing" the flow (Mar 1959). Several small flexible plastic streamers (5–10 cm) attached to the front swimming tunnel screen served to discourage fish from "nosing" up to the screen and thus blocking the water flow profile. At the rear of the swimming tunnel another screen prevents the fish from being sucked back into the impeller.

For addition or removal of fish the entire anterior movable portion of the apparatus forward from the fixed rear dome-and-cone can be detached by means of loosening "quick-lock" clamps and sliding the entire front section forward. A trolley suspension system over the aquarium for the forward section makes this operation quite rapid and simple. Soft gaskets provide quick sealing when the "quick-lock" clamps are tightened.

Access to the sealed respiratory apparatus from the outside is by means of two 30 mm diameter tubes through the outside cylinder into the inside cylindrical swimming tunnel. Revolutions of a paddle wheel, electronic transducer speedometer inserted into either of these access tubes to any desired level within the tunnel provide a direct speedometer measure of water flow rates.

At the same time, impeller shaft revolutions per minute were available by readings from a stroboscopic revolution counter. The speedometer readings and the shaft rpm's correlated rather precisely, so that it was possible for direct shaft readings to be made and converted to cm sec^{-1} readings for water flow measurements without having the paddle wheel speedometer inserted during a run with a fish in the respiratory swimming tunnel. During a run the access tubes were fitted with plugs through which were capillary tubes to permit water sample withdrawals for oxygen analysis while the fish was swimming. Oxygen analyses were by means of the calibrated Radiometer as described above.

At each salinity level, from 3 to 9 runs were at the maximum sustainable swimming velocity over a period of about 1 to 2 hr, depending on the size of the fish, several runs were at various intermediate speeds, and several runs were at zero velocity. At 10, 40, and 45 ppt. salinity there were also several overnight (8–10) hr) runs at zero velocity to provide measurements of standard rates. In all cases "burst" swimming activities were avoided completely in order to obviate problems of anaerobic respiration.

Standard Metabolism

Oxygen consumption rates were obtained in two ways for the determination of the standard metabolic levels. From the data used in the determination of routine rates at 15, 25, 35 and 45 ppt salinity, the method suggested by Brett (1964) was used. For each salinity series, the oxygen consumption rates as mg O_2 kg^{-1} hr^{-1} were regressed against the swimming velocities; through the lowest rates (not the mean), the regression was extrapolated back to zero velocity, at which point the standard rate was estimated. Standard rates estimated in this manner were always below the average resting rate which corresponded to the zero velocity value of the observed regression through all the points.

The second method involved the determination of the O_2 consumption rates in the Blazka chamber for about 8–10 hours overnight at zero water velocity. After the initial O_2 determination, the impeller was shut down; at the end of such a run the water was circulated briefly before the second O_2 analysis was made. The rates for the overnight period were expressed also as mg O_2 kg^{-1} hr^{-1} and were used especially for the rates at salinities of 10, 40, and 45 ppt.

Calculations

Apart from conventional tabulations and plots of the various data and pertinent averages (geometric means in cases of logarithmic data), two statistical systems were used.

$$\hat{Y} = a + b_w X_w + b_x X_s + b_v X_v \quad ,$$

where

$\hat{Y}$ = expected rate of O_2 consumption in $\log_{10}$ mg O_2 hr^{-1};
a = constant;
X_w, X_s and X_v are the independent variables, respectively, for $\log_{10}$ weight in grams, salinity in ppt and velocity in lengths sec^{-1};
and
b_w, b_s and b_v are the respective partial regression coefficients.

This is the same procedure used by Wohlschlag and Juliano (1959), Wohlschlag and Cameron (1967), Wohlschlag and Cech (1970) and others. The regression calculation techniques are given in most statistical manuals, e.g. Snedecor and Cochran (1967) or in various pretested library computer routines.

The second system of analysis for salinity-metabolism relationships at maximum sustained activity levels was to calculate the relationship between the $\log_{10}$ mg O_2 kg^{-1} hr^{-1} and the salinities in quadradic, cubic and quartic forms. The methods are given in the same references used for calculations of multiple regressions.

TABLE 1.

Cynoscion nebulosus. Swimming speed, respiratory metabolism, and scope for activity data at various salinities and 28°C.

Salinity (ppt)	Observed Max. X_v (L sec^{-1})	Avg. Max X_v (L sec^{-1})	Observed Max. $X_v \sqrt{L}$	Avg. Max. $X_v \sqrt{L}$	Max. mg O_2 kg^{-1} hr^{-1}	Avg. Max. mg O_2 kg^{-1} hr^{-1}; (N)	Standard mg O_2 kg^{-1} hr^{-1}	Scope for Max. Activity mg O_2 kg^{-1} hr^{-1}	Avg. Routine x_v mg O_2 kg^{-1} hr^{-1}	Avg. Routine mg O_2 kg^{-1} hr^{-1}; N
10	3.346	3.041	17.062	15,871	574.1	523.6 (7)	213.6[4]	311.3	–	–
15	3.674	3.307	18.913	18.058	727.8	625.2 (5)	156.7[1]	468.5	1.182	372.4 (10)
20	3.992	3.646	20.278	19.390	741.3	677.6 (8)	119.4[1]	558.2	–	–
25	3.802	3.677	19.961	19.129	671.4	657.7 (3)	118.0[1]	539.7	1.055	285.1 (10)
30	3.446[2]	3.164	17.805[2]	16.844	502.3	461.3[3] (6)	147.6[1]	558.2	–	–
35	3.213	2.823	16.032	15.011	494.3	461.3 (9)	187.5[1]	306.8	0.838	369.0 (10)
40	2.889	2.712	15.011	14.063	512.9	468.8 (6)	230.1[4]	238.7	–	–
45	2.244	2.092	12.272	11.385	403.6	379.3 (5)	241.0[4]	138.3	1.176	399.9 (10)
45	–	–	–	–	–	–	248.3[1]	–	–	–

[1] Standard metabolism determined by Brett (1964) method at 15, 25, 35, 45 ppt and extrapolated between. Data from routine determinations in annular metabolism chamber.
[2] Value of high swimming rate omitted for one fish "sheltered" in Blazka chamber.
[3] Values low due to poor condition of fish.
[4] Data from Blazka chamber at $X_v = 0$ overnight for 8–10 hours.

RESULTS

For the 10–45 ppt salinity range, the single maximum swimming rate at each salinity and the averages of the several maximum sustained velocities are in Table 1. Velocities are expressed as U cm sec^{-1} divided by L cm total length (Lengths $sec^{-1} = X_v$) or as $U/\sqrt{L} = cm\ sec^{-1}L^{-½} = (X_vL^{½})$. For each of the salinities, Table 1 lists the respective oxygen consumption rates as mg O_2 kg^{-1} hr^{-1} at the single maximum swimming rate, the average for maximum sustained swimming rates, the average routine rate with the corresponding swimming velocities, and the standard rates. The numbers of determinations are in parentheses where pertinent. Note that the rates of oxygen consumption are averaged from log rates; hence the averages are geometric means. Also in Table 1 are the scope values for each salinity. The footnotes explain additional attributes of the data in Table 1.

Multiple regressions between adjacent 5 ppt salinity levels for the data at maximum swimming rates as determined with the Blazka apparatus are in Table 2. Because the respiration rates at 30 ppt were very low and the fish in poor condition, an additional equation (5) utilizing 25 and 35 ppt data permitted a better estimation of 30 ppt rates. For all the equations in Table 2, the statistical significance of the overall equations, the weight coefficients b_w, and the swimming speed coefficients b_v are all high ($P < 0.001$); only the coefficients b_s for salinity are not significant, except for Equation (2), because of the great variability among individual fish and the small salinity ranges.

The relationships to salinity among metabolic rates at maximum sustained velocities, at routine swimming rates, and at standard rates are compared in the top panel of Figure 1. In this figure the heavy points are for the averages (geo-

TABLE 2

Multiple regression equations for oxygen consumption rates at 5 ppt salinity ranges. *Cynoscion nebulosus* data from Blazka chamber 28°C experiments including maximum sustained swimming velocities. July–October 1976.

Salinity Range (ppt)	N	Expected Log mg O_2hr^{-1}		Constant	Log Wt. X_w (g)	Salinity X_s (ppt)	Velocity X_v (L sec^{-1})	Multiple Correlation	Equation
10–15	45	$\hat{Y}$	=	=0.7810	+0.9910X_w	+0.0108X_s	+0.1271X_v	0.98	1
15–20	48	$\hat{Y}$	=	0.5705	+0.9952X_w	−0.0073X_s	+0.1491X_v	0.98	2
20–25	36	$\hat{Y}$	=	−0.8035	+1.0122X_w	+0.0015X_s	+0.1555X_v	0.98	3
25–30	26	$\hat{Y}$	=	−0.8196	+1.1123X_w	−0.0044X_s	+0.1269X_v	0.96	4
25–35	26	$\hat{Y}$	=	−0.9233	+1.1407X_w	−0.0045X_s	+0.1445X_v	0.97	5
30–35	32	$\hat{Y}$	=	−1.1379	+1.2364X_w	−0.0033X_s	+0.1236X_v	0.95	6
35–40	37	$\hat{Y}$	=	−1.559	+1.1699X_w	+0.0126X_s	+0.1285X_v	0.96	7
40–45	37	$\hat{Y}$	=	−0.3898	+1.0111X_w	−0.0067X_s	+0.1067X_v	0.98	8

metric means) of the several maximum rates at each salinity level; the arrow indicates the depressed value at 30 ppt. At each salinity and at the average weights and average maximum swimming velocities (Table 1) on which the heavy points are based, the appropriate equations from Table 2 provide estimates of the corresponding values plotted in the numbered squares. Also in the top panel of Figure 1 are the data for routine metabolic rates (triangles) and standard rates (diamonds). The scope values at each salinity are in the bottom panel of Figure 1.

Plots of swimming velocities against salinities are in Figure 2. The upper panel is for average maximum swimming rates in lengths sec^{-1} (upper line, heavy points) and for routine swimming rates (lower line, triangles). The bottom panel is for the average maximum swimming rates in lengths sec^{-1} times the square root of lengths (*i.e.*, cm sec^{-1} divided by the square root of lengths) plotted for the average maximum swimming rates against salinity (lower line, heavy points), for the single maximum rate at each salinity (upper line, squares), and for the individual small fish that "sheltered" itself against the upstream screen by "blocking" the flow of water through the chamber to reduce the "effective" rates far below the observed rate (labeled square in lower panel). A good explanation of the "flow blocking" anomaly is in Webb (1975).

For calculations of equations relating metabolism at maximum swimming rates to salinities at various orders, 43 datum points were used. (Because of the depressed metabolism, the 6 points at 30 ppt were eliminated.)

For the fourth order, the oxygen rate of consumption equation for $\hat{Y}$ kg^{-1} over X_s salinities (ppt) is

$$\hat{Y}\ kg^{-1} = 1.9943 + 0.12156\,X_s - 6.0960\,x10^{-3}\,X_s^2 + 1.2302\,x10^{-4}\,X_s^3 - 9.1230\,x10^{-7}\,X_s^4.$$

The plot of this line is very close to the visually drawn line in Fig. 1.

For the comparable cubic relationship,

$$\hat{Y}\ kg^{-1} = 2.2956 + 6.2509\,x10^{-2}\,X_s - 2.2477\,x10^{-3}\,X_s^2 + 2.2356\,x10^{-5}\,X_s^3,$$

which has a pertinent root at an optimal salinity of 19.6 ppt.

For the comparable quadratic relationship,

$$\hat{Y}\ kg^{-1} = 2.2956 + 1.8223\,x10^{-2}\,X_s - 4.4284\,x10^{-4}\,X_s^2,$$

which has a root of 20.6 ppt as an optimum salinity.

DISCUSSION

From the results above, it is clear that optimal salinity levels for *Cynoscion nebulosus* are the order of 20 ppt. at 28°C. From observations over several years of sustained south Texas coastal and estuarine collecting from hypersaline Baffin Bay to brackish San Antonio Bay, it was obvious that *C. nebulosus* were essentially unavailable below 10 and above 45 ppt salinity in collecting by seines, gill nets, and hook-and-line fishing. These observations agree in general with

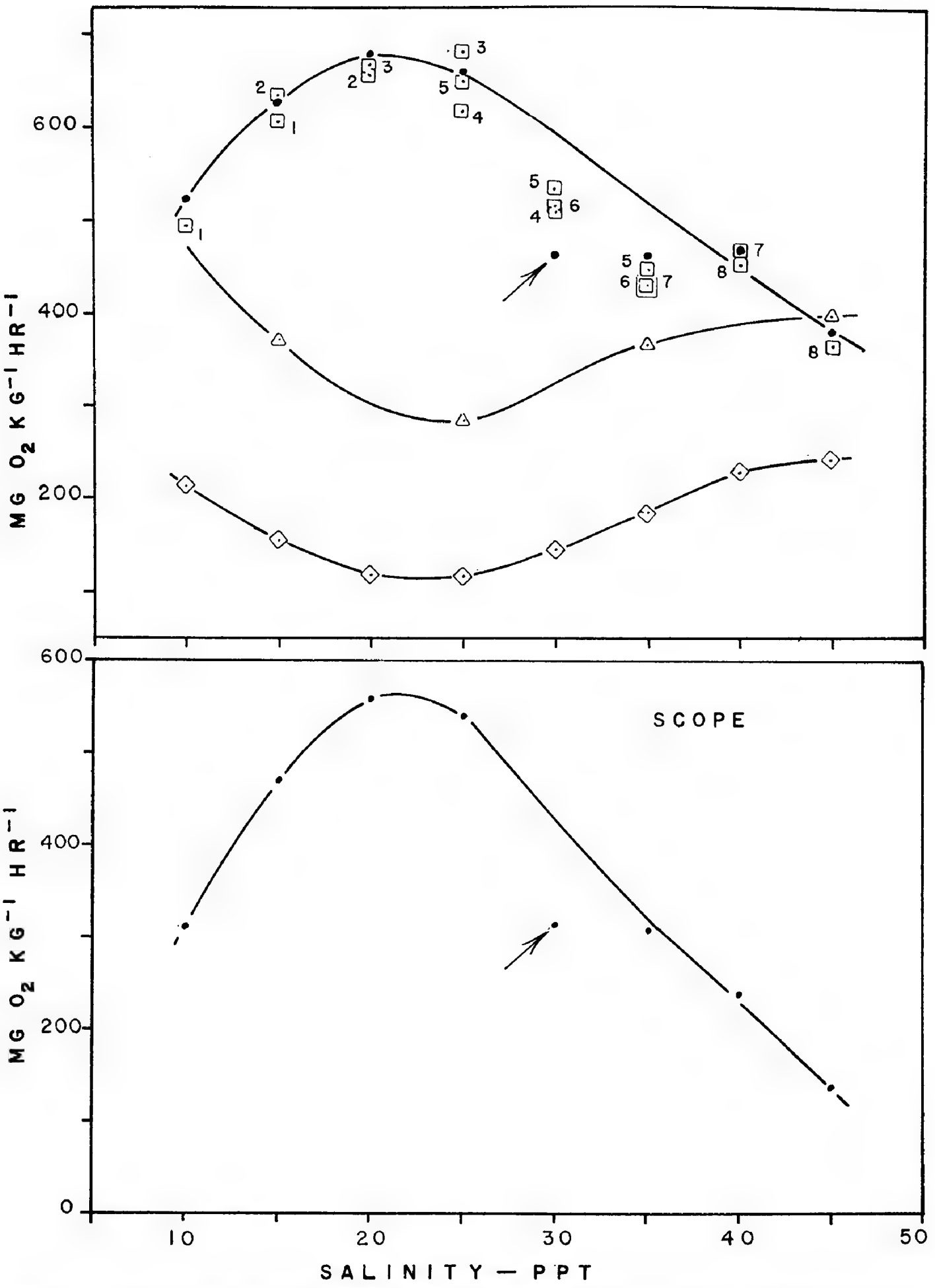

FIG. 1. Upper panel—Metabolism of *Cynoscion nebulosus* at standard (lower line, diamonds), routine (middle line, triangles) and at maximum sustained activity levels (upper line, heavy points) over a range of salinities at 28 C; maximum sustained rates calculated from equations in Table 2 in numbered squares. Lower panel—Scope for maximum sustained activity over salinity range. Arrows indicate "depressed" values from fish in poor condition. Fish were fully acclimated to each of the salinities.

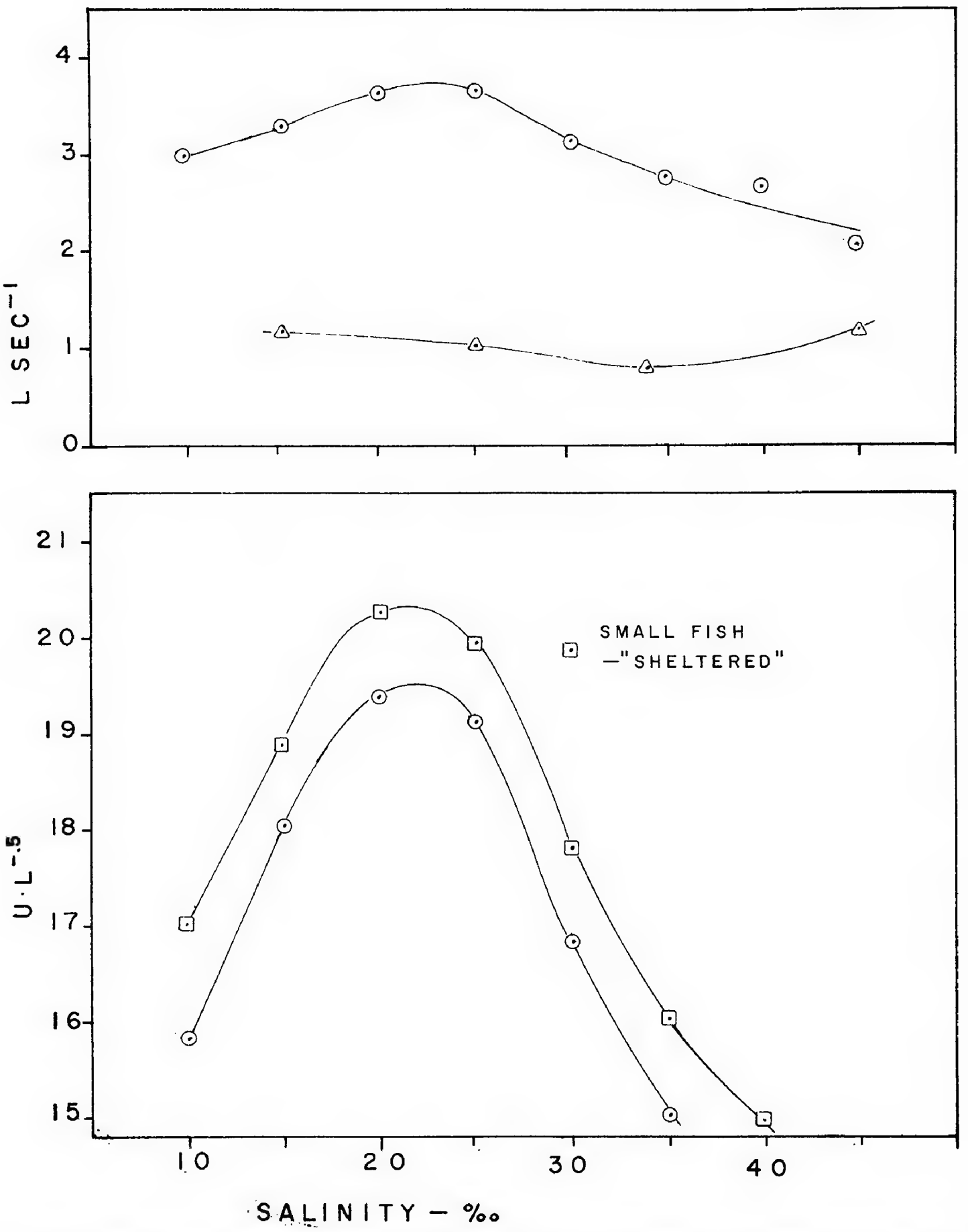

FIG 2. Swimming characteristics of *Cynoscion nebulosus* at different salinities. Top panel—Swimming speeds in body lengths (cm) sec^{-1} (upper line through heavy points); routine speeds (lower line through triangles). Bottom panel—Swimming speeds as cm sec^{-1} length $^{-0.5}$ (or length sec^{-1} times length$^{0.5}$) for average maximum rates (lower line through heavy points) and for maximum rate for single fish at each salinity (upper line through squares). Note that a realistic swimming rate for one small fish that "sheltered" itself at bottom front of chamber to "block" or reduce effective flow rate would be far below measured rate. Fish were fully acclimated to each of the salinities at 28° C.

published life history information, *e.g.*, Guest and Gunter (1958), Tabb (1966) for well aerated waters.

It is known first that temperatures of open estuarine and bay waters in the south Texas area are near, or slightly above, 28°C for as many as six months of the year, during which oxygen levels are fairly high (except in very shallow grass flats where there is natural depletion at night); and, second, that by late summer there tends to be a suppression of growth and metabolism (Cech and Wohlschlag 1975). In preliminary work it became apparent that (a) temperatures in the laboratory above 30° C were definitely less than optimal, (b) undernourished fish in poor condition were metabolically depressed at all temperatures and salinities, and (c) the fish during a week or so in holding tanks were visibly distressed and did not survive well above salinities of 45 and below 10 ppt. Accordingly, the study pertains to near saturation oxygen levels, to 28 ± 0.1° C for healthy fish in good condition (with possible exceptions noted), and for a salinity range of 10–45 ppt.

Standard Metabolic Rates

The determination of standard rates is rather difficult, even with carefully acclimated fish. Fry (1957, 1971) reviews the subject in detail in regard to fasting, spontaneous (non-locomotory) activity, and length of time at various laboratory acclimation regimes. In this study the fasting time of at least 48 hr seemed adequate, inasmuch as fish fasted for 72 hr or longer did not show any appreciably different oxygen consumption rates. Schalles and Wissing (1976) indicate that 48 hr fasting periods at higher natural summer temperatures are reasonable. The problem of the respiratory rate elevation (often to routine levels) by spontaneous activity is best circumvented by making determinations over longer periods of time, preferably at night, as was done over 8–10 hr periods in the Blazka chamber (Table 1). The Brett (1964) extrapolation method seems quite reasonable and consistent with the measurements in the Blazka chamber (Table 1 and Fig. 1). (In another study on this species, the use of flow-through respirometers for overnight periods gave standard rates that were remarkably near those of this study, which suggested that localized oxygen depletion in the static waters of the Blazka chamber caused no complications.) It thus appears that the standard rates are reasonable. That the standard rates are minimal at about 20 ppt salinity and about double at the 10 and 45 ppt extremes represents a pattern to be expected from other studies on isosomotic levels and salinity effects on metabolism (Rao 1968, 1969; Nordlie and Leffler 1976) with the respiratory rates near a minimum at isosmotic conditions. Whether about 20 ppt salinity is the true isosmotic point for *Cynoscion nebulosus* has not been determined. For both this species and the local stiped mullet, *Mugil cephalus* (isosmotic point at about 10 ppt), the standard metabolic level is approximately double the minimal rate when salinities are at about 45 ppt (Nordlie and Leffler 1976).

Routine Metabolic Rates

Exactly what constitutes a reasonable estimate of routine rates is somewhat more problematical, inasmuch as standard rates determined at zero swimming speeds are often as high due to spontaneous activity or recency of feeding with high specific dynamic action (Fry 1957, 1971). However, with many species like *C. nebulosus*, general observations in both nature and in the annular type of chamber are that a speed of about one body length sec^{-1} is realistic. This routine speed of 1 L sec^{-1} is also theoretically realistic (Weihs 1973). For the annular chamber at lesser rates, there tends to be more spontaneous activity and general irritability than in nature; at higher rates that are forced, there tends to be a more "labored" swimming effort than appears at high rates either in nature or in the Blazka chamber. Visually subjective behavioral guidelines for these tendencies are thus good non-quantitative indicators for determining whether or not a routine swimming rate is rational with respect to observations in nature. (Incidentally, it did not appear possible to identify a consistent routine rate between zero and nearly 4 L sec^{-1} rates in the Blazka chamber.) In any case the routine respiratory metabolism rates are roughly double those at the standard level over the salinity range in this study.

The fact that the routine metabolism of *Cynoscion nebulosus* at swimming speeds of about 1 L sec^{-1} is about double the standard metabolism is in general agreement with Winberg (1965), Mann (1969) and Kerr (1971). From an ecological viewpoint, the routine rate under normal feeding conditions might be considered a more or less normal operational level for *C. nebulosus* and other species that cruise at about 1 L sec^{-1} during foraging. In the laboratory tanks, the seatrout, when feeding on live shrimp, a common natural food (Guest and Gunter 1958; Tabb 1966), "cruise" at slightly less than 1 L sec^{-1} while feeding and then tend to become quiescent for several hours to several days, during which time assimilation energy requirements along with behavioral functions such as expressed by spontaneous activity might also be about equal to the energy required for foraging (Kerr 1971). The "routine" metabolic level that is high enough to allow for both foraging and normal weight maintenance could be considered to be the ecological maintenance level (Brett 1976); by contrast the standard level is the physiological maintenance level. The distinction between these levels can be of major concern in interpreting the ecological pertinence of physiologically oriented data (Holeton 1974).

Metabolism at Maximum Sustained Activity

When the various averages of the maximum metabolism rates at each salinity are plotted as in Fig. 1, it is apparent that the optimum (maximum) is at about 20 ppt as is the optimal scope for maximum activity. At the average maximum activity and weight for each salinity the numbered multiple regression equations in Table 2 yield the respective calculated maximum values (in numbered squares) shown in Fig. 1. At 30, and probably 35, ppt salinity both the observed and calculated values appear quite low. For the 6 depressed metabolism

values at 30 ppt, the log weight-log length plots of the individual fish lay along a line with a slope of about 1.9, which was derived from other data on definitely starved fish, among which the largest showed the greatest weight depression; ordinarily such plots for healthy fish in good condition would have a slope of about 2.9 (from data of Guest and Gunter 1958 and from data in preparation). Equations 4 and 6 are definitely biased downward when used for calculated values at 30 ppt. Depression of this sort agrees with Fry's (1947) original premise of depression in active metabolism under stress.

An important feature of the equations in Table 2 is that the weight-metabolism coefficient near unity is rather higher than those of about 0.8 for most published data. There are probably hydrodynamic explanations for the high metabolism-weight coefficients, which involve both the highest swimming velocities and the size of the fish that range upward to sizes larger than those used in most studies (Brett 1965, Webb 1975). Interestingly, the swimming-metabolism coefficients tend to decline slightly toward the salinity extremes of 10–15 ppt and 40–45 ppt. A further detailed study on hydrodynamics related to this apparent anomaly is being prepared by the junior author. From Table 1 and Fig. 2, the conventional plots of either L lengths (cm) sec^{-1} (X_v) or in cm sec^{-1} $length^{-0.5}$ (i.e. $X_v^{0.5}$) also show maxima at about 20 ppt when plotted either as averages or as the single maximum value at each salinity. The swimming velocity data plotted against salinities could be used directly to determine the optimal salinity for *Cynoscion nebulosus*, a procedure that is direct and simple and that does not require the more involved Blazka chamber for O_2 consumption rate measurements.

The use of the cubic and quadratic equations for all the data at maximum sustained velocities (dependent variable) over the range of salinities (independent variable) by maximization for the optimum salinity value provides a good check. In the case of Fig. 1, the quartic equation yields estimated metabolic values at the various salinities along a line that very closely approximates the visually drawn line for average maximum metabolism, while the lower order equations agree nearly as well. However, these lines are calculated without the 30 ppt depressed metabolic data, and some caution should be used in interpreting the lines since the data are not strictly "orthogonally" balanced with respect to numbers in subsets, weights or salinity range intervals.

From a general ecological and zoogeographical standpoint, the fact that the routine and active levels are about equal at about 10 and 40–45 ppt salinity indicates that there may be no excess available energy beyond ecological maintenance requirements at these salinity extremes. Because the spotted seatrout do not usually persist in the south Texas coastal waters below or above these salinity levels, the plots of routine and active metabolism against a salinity range (as in Fig. 1) suggest that the salinity levels at which routine and active metabolic rates are about equal are useful in determining zoogeographic ranges on the basis of energetics. In turn, energy appears to be a common denominator for evaluating environmental optima and stress effects in the sense of Cody (1974), in determining population growth-foraging relationships in the sense of Kerr (1971), or in determining metabolic or respiration effects that are highly sensitive for

heterotrophs in ecosystem models in the sense of O'Neill (1976), as well as in determining metabolic scope for metabolism and growth from Fry's (1947) original concept in the sense of Brett (1976).

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LITERATURE CITED

BEAMISH, F. W. H. 1964. Respiration of fishes with special emphasis on standard oxygen consumption. *Can. J. Zool.* **42**:177–188.

BLAZKA, P., M. VOLF and M. CEPELA. 1960. A new type of respirometer for the determination of metabolism of fish in the active state. Physiol. Bohemoslov **9**:553–558.

BRETT, J. R. 1958. Implications and assessments of environmental stress. *In*: P. A. Larkin (ed.), *The investigation of fish-power problems.* The H. R. MacMillan lectures in fisheries. Univ. British Columbia, Vancouver, p. 69–83.

————. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Bd. Canada.* **21**:1183–1226.

————. 1965. The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). *J. Fish. Res. Bd. Canada.* **22**:1491–1501.

————. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *Am. Zoologist.* **11**:99–113.

————. 1976. Scope for metabolism and growth of sockeye salmon, *Oncorhynchus nerka*, and some related energetics. *J. Fish. Res. Bd. Canada* **33**:307–313.

————and N. R. Glass. 1973. Metabolic rates and critical swimming speeds of sockeye salmon (*Oncorhynchus nerka*) in relation to size and temperature. *J. Fish. Res. Bd. Canada.* **30**:379–387.

————, J. E. SHELBOURN and C. T. SHOOP. 1969. Growth rate and body composition of fingerling sockeye salmon, (*Oncorhynchus nerka*), in relation to temperature and ration size. *J. Fish. Res. Bd. Canada.* **26**:2363–2394.

CECH, J. J., and D. E. WOHLSCHLAG. 1975. Summer growth depression in the striped mullet, *Mugil cephalus* L. *Contr. mar. Sci.* **19**:91–100.

CODY, M. L. 1974. Optimization in ecology. *Science.* **183**:1156–1164.

FRY, F. E. J. 1947. Effects of the environment on animal activity. Univ. Toronto Studies Biol., Ontario Fish. Res. Lab. **69**:1–62.

————. 1957. The aquatic respiration of fish, p. 1–63. *In*: M. E. Brown (ed.), *The Physiology of Fishes*, Academic Press, New York.

———. 1971. The effect of environmental factors on the physiology of fish. p. 1–98. *In*: W. S. Hoar and D. J. Randall (eds.), *Fish Physiology*, Vol. 6, Environmental Relations and Behavior, Academic Press, New York.

GUEST, W. C. and G. GUNTER. 1958. The seatrout or weakfishes (Genus *Cynoscion*) of the Gulf of Mexico. Gulf States mar. Fish. Comm., Tech. Summary. **1**:1–40.

HOLETON, G. F. 1974. Metabolic cold adaptation of polar fishes: fact or artifact? *Physiol. Zool.* **47**:137–152.

KERR, S. R. 1971. A simulation model of lake trout growth. J. Fish. Res. Bd. Canada **28**: 815–819.

KLOTH, T. C. and D. E. WOHLSCHLAG. 1972. Size-related metabolic responses of the pinfish. *Lagodon rhomboides*, to salinity variations and sublethal petrochemical pollution. *Contr. mar. Sci.* **16**:125–137.

MANN, K. H. 1969. The dynamics of aquatic ecosystems. *Advan. Ecol. Res.* **6**:1–81

MAR, J. 1959. A proposed tunnel design for a fish respirometer. Pac. Nav. Lab., Esquimalt, B. C., Tech. Memo. **59**:1–13.

NORDLIE, F. G. and C. W. LEFFLER. 1976. Ionic regulation and the energetics of osmoregulation in *Mugil cephalus* L. *Comp. Biochem. Physiol.* **51A**:125–131.

O'NEILL, R. V. 1976. Ecosystem persistence and heterotrophic regulation. *Ecology*. **57**:1244–1253.

RANDALL, D. J. 1970. Gas exchange in fish, p. 253–292. *In*: W. S. Hoar and D. J. Randall (eds.), *Fish Physiology*, Vol. 4 The Nervous System, Circulation, and Respiration, Academic Press, New York.

RAO, G. M. M. 1968. Oxygen consumption of rainbow trout (*Salmo gairdneri*) in relation to activity and salinity. *Can. J. Zool.* **46**:781–786.

———. 1969. The effect of activity, salinity, and temperature on plasma concentrations of rainbow trout, *Can. J. Zool.* **47**:131–134.

SCHALLES, J. F. and T. E. WISSING. 1976. Effects of dry pellet diets on the metabolic rates of bluegill (*Lepomis macrochirus*). *J. Fish. Res. Bd. Canada.* **33**:2443–2449.

SNEDECOR, G. W. and W. G. COCHRAN. 1967. *Statistical methods.* Iowa State Univ. Press. Ames, Iowa.

TABB, D. C. 1966. The estuary as a habitat for spotted seatrout, *Cynoscion nebulosus. In*: A symposium on estuarine fisheries. *Am. Fish. Soc. Spec. Publ.* **3**:59–67.

WEBB, J. W. 1975. *Hydrodynamics and energetics of fish propulsion. Bull. Fish. Res. Bd. Canada* No. **190**, 159 pp.

WEIHS, D. 1973. Optimal fish cruising speed. *Nature.* **245**:48–50.

WINBERG, G. G. 1956. Rate of metabolism and food requirements of fish. *Trans. Ser. Fish. Res. Bd. Canada* **194**:x + 1–158.

WOHLSCHLAG, D. E. and R. O. JULIANO. 1959. Seasonal changes in bluegill metabolism. *Limnol. Oceanogr.* **4**:195–209.

———, and J. N. CAMERON. 1967. Assessment of a low-level stress on the respiratory metabolism of the pinfish (*Lagodon rhomboides*), *Contr. mar Sci.* **12**:160–171.

———, J. N. CAMERON and J. J. CECH. 1968. Seasonal changes in the respiratory metabolism of the pinfish (*Lagodon rhomboides*). *Contr. mar. Sci* **13**:89–104.

———, and J. J. CECH. 1970. Size of pinfish in relation to thermal stress response. *Contr. mar. Sci.* **15**:22–31.